

A PALEOLIMNOLOGICAL STUDY OF ELK LAKE IN
ITASCA STATE PARK, CLEARWATER COUNTY, MINNESOTA

[v. 1]

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DONNA MARGARET IRENE STARK

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ITASCA STATE PARK, CLEARWATER COUNTY, MINNESOTA

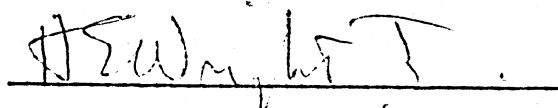
The main objective of the Elk Lake study is to interpret the limnological history of Elk Lake through a study of fossil aquatic organisms in nine sediment cores. Fossils of chironomids, ostracods, molluscs, aquatic plants and diatoms were examined in the cores and quantitative stratigraphies of individual taxa were graphed. Five faunal units were established on the basis of the stratigraphy of the 69-5 core, which was taken near the middle of the lake. These faunal units were also applied to the shallow-water cores by correlating their pollen stratigraphy with that of the 69-5 core.

In order to aid in the interpretation of the faunal units, two kinds of supporting studies were undertaken. Ecological studies of ostracods and molluscs living in surface sediments, in open water, and in association with aquatic plants were carried out. A study was also designed to determine the extent of redistribution of fossil remains of ostracods, molluscs, chironomids and seeds in Elk Lake. Samples of surface sediment were taken in a transect across the lake and fossils were counted in given volumes of sediment. The extent of redistribution of fossils after death was determined by comparing the distributions of fossil and living organisms. It was found that fossils of many littoral organisms are transported offshore by wave-induced currents and deposited in a shell zone located at a depth of 2-10 m. Some littoral organisms are transported to some extent into deeper waters, probably by water movements within the epilimnion or by floating on the water surface. Most benthic organisms living in

relatively deep water seem to undergo little transportation by water currents but are preserved in situ.

The paleolimnology of Elk Lake is discussed with respect to the five faunal units recognized in the stratigraphic study. Unit A represents the period in which Elk Lake was receiving clastic sediments, presumably derived from the erosion of glacial deposits of the St. Louis sublobe. Few fossils of chironomids, molluscs and seeds were found in the sediments but several cold-hardy ostracods were identified. Pollen analysis places unit A in the Herb (?) and lower Picea pollen zones. Fossils of chironomids, molluscs and ostracods suggest that Elk Lake was oligotrophic during the period represented by unit B, which extends to the end of the Pinus banksiana/resinosa-Pteridium pollen zone. Unit C, which corresponds to lower and middle Quercus-Gramineae-Artemisia pollen zone, may represent a period of increased productivity in Elk Lake since fossils of chironomids, molluscs and ostracods suggest lowered oxygen content of Elk Lake waters. An abrupt decline in abundance of all ostracod species in deep water marks the beginning of unit D, which is interpreted as a period of decreased productivity in Elk Lake. Unit E, which begins in the middle of the Quercus-Ostrya pollen zone, seems to represent a period of eutrophication in Elk Lake. The stratigraphy of chironomids, molluscs, ostracods, and diatoms suggests an increase in productivity at the base of this unit. The increased percentage of organic matter in the sediment and the higher sedimentation rate seem to confirm this suggestion. Subunit E' is delimited at the top of unit E by an abrupt darkening of sediments in shallow water and by a change from fine laminations to broad, poorly defined bands in deep water.

Stratigraphy of chironomids, ostracods and diatoms suggests abrupt eutrophication at the base of this subunit, followed by partial reversion to pre-disturbance conditions. It is suggested that eutrophication of the lake resulted from the inwash of soil as the 1-m dam built at the outlet of Elk Lake at Chambers Creek in 1917 raised the water level.

A handwritten signature, likely "J. S. Wright", written in dark ink above a horizontal line.

Major Advisor

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INTRODUCTION

Location and Description

Elk Lake is located in Itasca State Park, Clearwater County, northern Minnesota (Fig. 1). It flows into the southern end of the west arm of Lake Itasca through Chambers Creek. It is roughly oval in shape and is slightly greater than one mile long in a northwest direction (Fig. 2). The main feature of the bottom topography is the division of the basin into two depressions, 69 ft and 97 ft in depth, separated by a ridge that is about 37 ft below the water surface. A submerged bench occurs around the periphery of the lake at a depth of about 9 ft.

The sediments of Elk Lake are mainly sand and organic mud near the shore, coarse materials on the bench, and a very dark gyttja (organic ooze) in the rest of the basin. The water chemistry places the lake in the category of hard-water lakes (alkalinity 90-150 ppm, summer pH of surface waters 8.0-8.8), which are common on the calcareous gray glacial drift that covers much of central and northern Minnesota (Moyle, 1945). With respect to organic productivity, Elk Lake may be classified as "mesotrophic" (Baker and Davison, unpub. man.).

Geology

Two lobes of the continental ice sheet of the Wisconsin glaciation contributed to the deposits that form the basin of Elk Lake. The basin of Elk Lake is presumably part of a former subglacial tunnel-valley system, including also the three arms of Lake Itasca, which was formed by streams beneath the Wadena lobe when it stood at the Itasca moraine (about 16,000 years ago according to Wright and Ruhe,

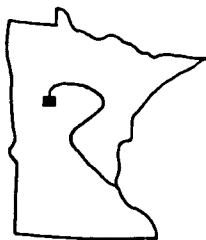
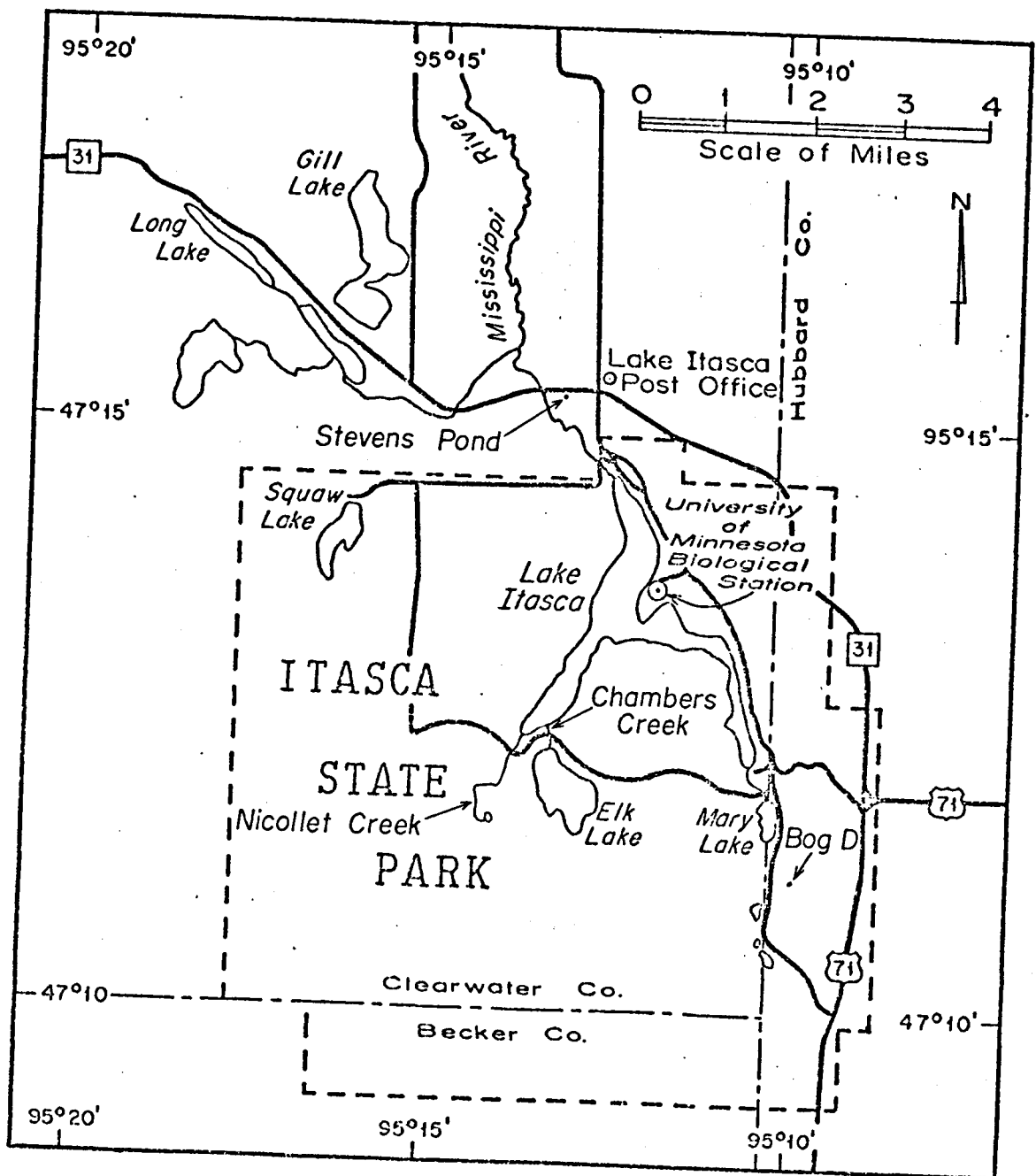


Fig. 1. Itasca State Park and vicinity
(modified from Megard, 1967).

Location: Sec. 22, T. 143N., R. 36W.

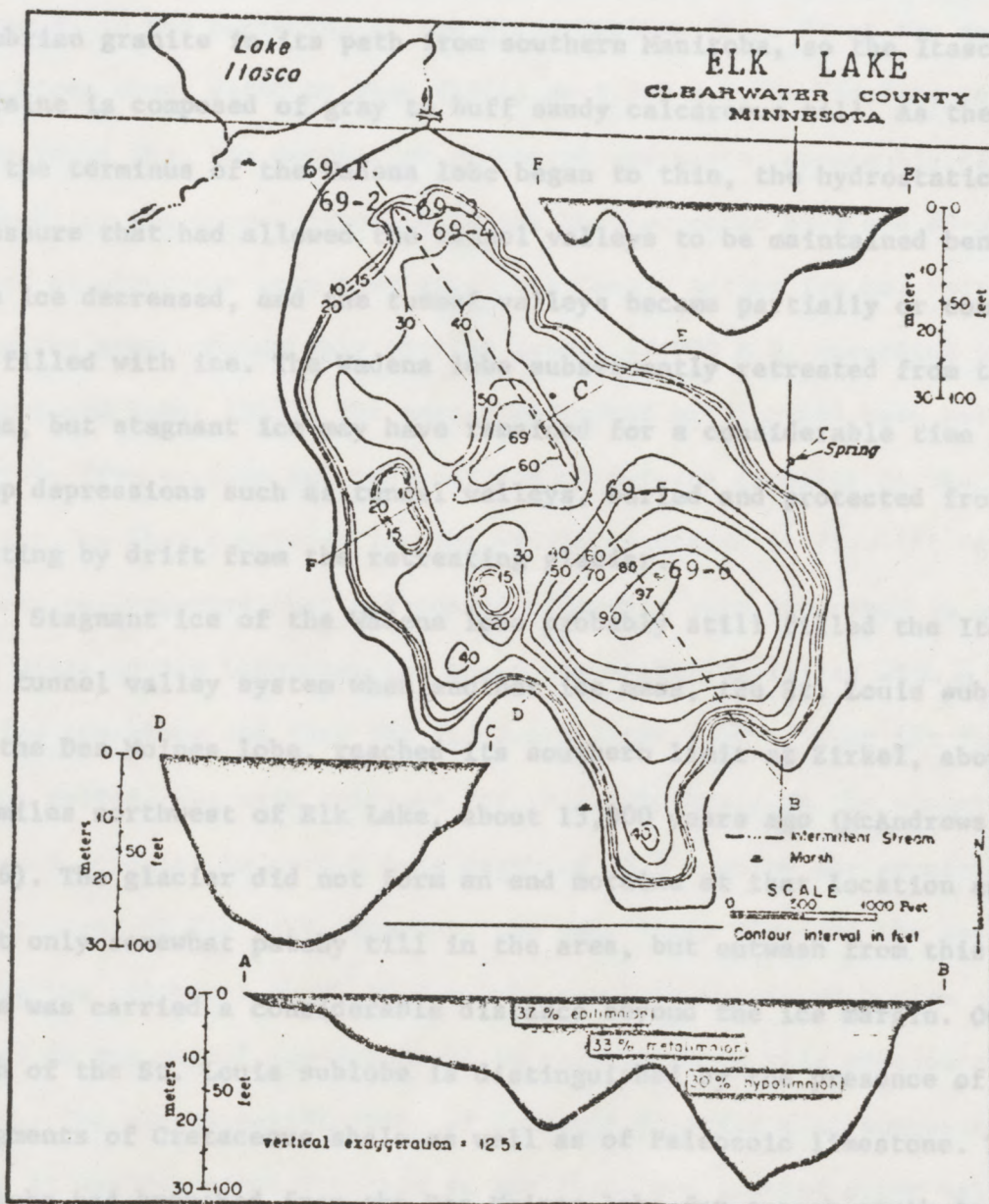


Fig. 2. Contour map of Elk Lake, showing locations of long cores and the transect of surface-sediment samples (dashed).

1965). The Wadena lobe had encountered Paleozoic limestone and Precambrian granite in its path from southern Manitoba, so the Itasca moraine is composed of gray to buff sandy calcareous till. As the ice at the terminus of the Wadena lobe began to thin, the hydrostatic pressure that had allowed the tunnel valleys to be maintained beneath the ice decreased, and the tunnel valleys became partially or completely filled with ice. The Wadena lobe subsequently retreated from this area, but stagnant ice may have remained for a considerable time in deep depressions such as tunnel valleys, buried and protected from melting by drift from the retreating glacier.

Stagnant ice of the Wadena lobe probably still filled the Itasca-Elk tunnel valley system when another ice mass, the St. Louis sublobe of the Des Moines lobe, reached its southern limit at Zirkel, about 16 miles northwest of Elk Lake, about 13,000 years ago (McAndrews, 1966). The glacier did not form an end moraine at that location and left only somewhat patchy till in the area, but outwash from this ice lobe was carried a considerable distance beyond the ice margin. Outwash of the St. Louis sublobe is distinguished by the presence of fragments of Cretaceous shale as well as of Paleozoic limestone. The sublobe had branched from the Des Moines lobe far enough south to erode Cretaceous shales from northwestern Minnesota. Shale-bearing outwash deposits have been identified in a gravel pit near the post office at the north edge of Itasca Park and in the basal sediments at the bison site at Nicollet Creek. (Shay, 1971).

The basal sediments of Elk Lake also contain shale fragments derived from erosion of outwash deposits, if not deposited directly in outwash from the St. Louis sublobe. Direct deposition of outwash is unlikely because the deposition of the coarse sediment ended about

9,500 B.P. (The upper boundary of coarse sediment in each core corresponds to the beginning of the Picea decline (Fig. 3) at the end of the Picea zone, dated by Shay (1971) as 9,500 B.P. In Nicollet Valley, Shay found that the deposition of coarse sediments, apparently closely resembling the coarse deposits in the shallow cores 69-2 and 69-3, ended at about the same time as in Elk Lake). Active ice had retreated from the area considerably earlier (about 12,000 B.P. according to Wright and Ruhe, 1965). The coarse sediments may instead have been derived from erosion and redeposition of outwash deposits in the vicinity, as Shay concluded for the similar deposits in Nicollet Valley. It may be suggested that the coarse sediments were deposited in shallow water in Elk Lake when the basin was partially filled with a buried ice block and that the sediments later lowered when the ice block melted. The main evidence for this hypothesis is the occurrence of sand deposits in core C to a depth of 16.3 m below the present water level of Elk Lake. However, the very steep slope of the basin along the northeast shore of Elk Lake may have permitted bottom currents in the normal ice-free lake to carry sand to this considerable depth. The microstratification of the sand deposits also suggests that it was deposited directly in the lake, not lowered after melting of an ice block (unless lowered gradually without much disturbance).

Vegetation

Elk Lake is located in the Pine-Hardwood forest, which is a transitional zone between the northern coniferous forests and the temperate deciduous forests, for elements of both are present — Abies balsamea, Picea glauca, P. mariana, Pinus spp., and Betula papyrifera from the northern boreal forests, and Quercus borealis,

Acer rubrum, Betula lutea, Acer saccharum, Ulmus spp., and Tilia americana from the deciduous forests (Grant, 1934; Janssen, 1967; McAndrews, 1966). There has been considerable discussion relative to the successional status of the vegetation of the Pine-Hardwood zone, especially with respect to the pine forests. Most ecologists recognize that most of the stands of pine forest form an edaphic subclimax on the poorer sandy soils of the uplands (McAndrews, 1966; Grant, 1934). Other ecologists emphasize the role of fire in establishing and maintaining the pine stands of the Pine-Hardwood forests. Studies of fire history in Itasca State Park seem to confirm this opinion, for the major portion of the magnificent red pine stands of the Park date back to specific periodic fires (Frissell, 1968).

Human influence on the natural vegetation of Itasca State Park has been reviewed in considerable detail by Dobie (1959). The effects of Indians, explorers, and early settlers was probably negligible in comparison with the devastation wrought by the logging operations in the park, which were carried out between the years 1901 and 1921. Natural vegetation was usually left along lake shores, but extensive areas of pine forest were logged behind these fringe belts. In the case of Elk Lake, vegetation on the slopes immediately surrounding the lake consists mainly of balsam fir, with a red pine overstory on the western shore of the lake. Back from the shore, stands of aspen and birch now cover most of the area that was logged earlier in the century (Meyer and Jensen, 1966).

Objectives

The main objective of the present study was to obtain information

concerning past limnological conditions in Elk Lake through a study of fossil aquatic organisms in a series of sediment cores. The aquatic organisms considered in the stratigraphic study included ostracods, molluscs, chironomids, aquatic macrophytes, and diatoms. Ecological studies of several of the present-day forms were undertaken to supplement the ecological information available in the literature. But even a knowledge of the ecological significance of a particular species found in a core is often insufficient evidence upon which to base an interpretation of past ecological conditions. Particularly if past water depth is to be estimated on the basis of the presence of a fossil in a core, it is necessary to know whether the organism actually lived in situ or whether it was transported to this location and deposited after it died. Thus studies were designed to determine also the extent of redistribution of fossil remains of most of the above-mentioned groups of aquatic organisms in Elk Lake.

Stratigraphic correlations among the several Elk Lake sediment cores were made on the basis of pollen and sediment stratigraphy, which also contributed information concerning past ecological conditions in the watershed and in Elk Lake. Pollen analysis also permitted a correlation between limnological changes in Elk Lake and changes in the terrestrial environment of the region, as well as providing an approximate timescale for the Elk Lake cores through the close comparison of pollen stratigraphy of Elk Lake cores with dated pollen profile of nearby Bog D.

Acknowledgments

The assistance of several people has been greatly appreciated in the present study. I am especially indebted to Dr. H. E. Wright, Jr.

for his kindly direction throughout the course of the research and writing. Others have given valuable aid in identification of fossils and discussion of ideas: R. C. Bright in seeds, molluscs and diatoms, W. A. Watts in seeds, F. M. Swain in ostracods, R. O. Megard in chironomids, J. P. Bradbury in diatoms and E. J. Cushing in pollen. For help in field work I am grateful to many, including R. G. Colingsworth, A. L. Baker and M. C. Whiteside. In the laboratory, assistance was given by Jean Waddington and Orin Anderson.

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METHODS

Stratigraphic Studies

The stratigraphic studies in Elk Lake were carried out on seven long cores and two short cores obtained from the lake between 1968 and 1970. The long cores were collected in the winters of 1968 and 1969, with a modified Livingstone sampler having a core tube of 5-cm diameter. Most of the long cores were obtained in one-meter segments, which were extruded, wrapped in saran wrap and aluminum foil, and labelled in the field. An 11-meter core tube, designed by H. E. Wright, was used in the collection of the upper part of the Elk 69-6 core. A drive of 855 cm was made with this core tube, and the core was extruded and cut up into segments approximately one meter in length, which were wrapped and labelled as described above. This "continuous core" method was used to collect the 69-6 core in deep water in order to permit accurate counting of the laminae that had been earlier observed in a short core taken from Elk Lake in deep water. The locations of the seven long cores examined in the present study are shown in Fig. 2. Cores 69-1 through 69-6 were collected at intervals along a northwest-southeast transect, whereas core C was collected a short distance to the east of the transect.

Two short cores were collected in Elk Lake, one in relatively shallow water and the other in the deepest hole of the lake. The shallow-water short core was collected near the northern end of the northwest-southeast transect in water 775 cm deep. A one-meter plastic tube of one-inch diameter was used to obtain this core from a boat in the summer of 1969. The core was extruded in the laboratory in 1-cm segments, each segment being stored in labelled glass vials

until examined. The deep-water short core was collected in the winter of 1970 with a freezing technique designed to preserve the laminae in the soft surface sediments. A 7.5-cm casing tube with sealed lower end and lead weights was filled with 20 kg dry-ice pellets and 10 l butanol. The upper end was then sealed with a cap containing some vents to permit the escape of CO₂ gas. The corer was lowered rapidly until it penetrated the sediments. It was allowed to remain relatively undisturbed for about 30 minutes, during which time sediment in contact with the outer surface of the tube froze. The tube was then raised to the surface and the entire core was wrapped in aluminum foil.

The Elk Lake cores were sampled in the laboratory and the sediment samples prepared for examination by a variety of techniques, according to the type of organism to be studied. Pollen analysis was carried out on the seven long cores and the two short cores mentioned above. Sediment samples intended for use in pollen analysis were taken at intervals that varied considerably between cores, according to the purpose of the pollen study. In cores 69-5, 69-6, C, and the frozen short core, quantitative samples of 1-cc volume were taken, as measured by packing sediment in a bottle cap having a volume of 1ccc, so that calculation of absolute pollen frequency and influx could be made. In most cases the sediment samples were taken from about 1 cm of core length, but in the laminated cores an attempt was made to sample a definite number of annual laminations — 10 years in the 69-6 core and 4 years in the finely laminated portion of the frozen short core. These were homogenized, and 1-cc samples were taken from them in the manner described above.

Sediment samples were prepared for pollen analysis by a method modified from that of Faegri and Iversen (1964). The preparation usually included successive treatments with hot 10% KOH, hot 50% acetic acid, concentrated HCL, hot HF followed by dilution with 95% ethanol, hot concentrated HCL, and hot acetolysis solution. The pollen concentrate was stained with safranin, dehydrated with 100% ethanol, and mounted in silicone oil. If samples were intended for calculations of absolute pollen frequency, a measured volume, usually 1 ml, of a solution containing pollen grains of the exotic plant, Ailanthus altissima, was added before the preparation was begun. The exotic pollen was suspended in a solution of corn syrup, to which preservatives were added. The concentration of Ailanthus altissima grains in the prepared suspension was determined by making several counts of the pollen in a hemacytometer. Two concentrations were used in this study: 7.4×10^4 grains/ml (samples 1248-1448 in core 69-5) and 7.2×10^4 grains/ml (samples 1450-1625 in core 69-5 and all samples in 69-6 and SCF). The Ailanthus suspensions were mixed on a magnetic stirrer for approximately a half hour before samples were taken. Pollen was analyzed with a Nikon binocular microscope equipped with 10x oculars, 40x apochromatic objectives, and 100x fluorite objectives. Identifications of pollen grains were made by the use of keys in Faegri and Iversen (1964) and by comparison with reference pollen collections of the Limnological Research Center, University of Minnesota. In samples taken from the 69-5 core and frozen short core, 300 grains were counted in each sample, while in most of the other cores only 150 grains or fewer were counted in each sample, for the purpose was mainly to correlate sediment stratigraphy among cores. Pollen

diagrams were drawn for each core, showing percentages of each taxon calculated on the basis of the sum of all pollen grains (and spores in the 69-4 and 69-5 cores) counted in each sample.

In core 69-5, the number of Ailanthus grains recorded during a count of 300 fossil pollen grains is indicated on the diagram, giving an approximate measure of changes in pollen frequency. In each sample, the number of fossil grains in 1 cc of sediment (APF) was calculated by multiplying the number of fossil pollen grains counted in a sample by the factor A/a , where A is the number of Ailanthus grains added per 1 cc of sediment and a is the number of Ailanthus grains tallied during the counts of fossil pollen.

Absolute pollen influx values were calculated for two cores — the 69-6 core and the frozen short core. In the 69-6 core, laminae, apparently formed annually, were present in the upper 631 cm and in portions of the rest of the core. Counting of these yearly layers permitted calculation of average deposition times of each core segment (Table 3). The absolute pollen frequency values calculated for this core could be converted to absolute pollen influx values by dividing each APF value by the deposition time (yrs/cm) at the level from which the sample was taken. Absolute pollen influx was also calculated for the frozen short core, although only the lower part of the core has clearly definable laminae.

Sediment types indicated on the pollen and faunal diagrams were designated on the basis of qualitative examination of sediment color and composition. The composition was estimated both by microscopic examination, in which relative amounts of silt particles, organic matter, and marl fragments were estimated, and by macroscopic examination, in which the quantities of large marl fragments, stones, and

other remains were noted. The presence of calcium carbonate throughout most of the Elk Lake cores was confirmed by the reaction of 10% HCl on the sediments.

Besides this qualitative analysis of most of the Elk Lake cores, the sediments of the 69-5 core were examined by ignition studies designed to estimate the percentage of the dry weight contributed by calcium carbonate and organic matter. Approximately 5 cc of sediment were used in each sample. The wet sediment was placed in clean weighed crucibles and left in a drying oven overnight. The crucibles containing the dried sediment were then weighed again and the weights of the dried sediments calculated by subtracting the original weights of the crucibles. The crucibles were then placed in an oven at 625°C for 2½ hours, allowed to cool, and weighed to determine the weight loss during the ignition, which presumably represented the weight of organic matter. The crucibles were kept in the dehydrated atmosphere of a desiccator until weighing to prevent adsorption of water, which would increase their weight. The samples were then placed in an oven at 950°C for 30 minutes, and the weight loss was determined as above. The weight loss during this ignition period was assumed to represent loss of carbonates. The organic matter content and the carbonate content were then calculated as percentages of the original weight of the dried mud (Plate 2).

Deposition times were calculated for some of the Elk Lake cores. In the 69-6 core, the presence of laminae, which are presumably annual, permitted calculation of deposition times in parts of the core as described above. In Elk Lake cores 69-2, 69-5, and C, approximate deposition times were calculated by applying C¹⁴ dates from Bog D to

corresponding pollen-zone boundaries in the Elk Lake cores.

Most of the Elk Lake cores examined in the present study (all except 69-6) were sampled for fossil remains of aquatic organisms, including chironomid head capsules, mollusc shells, seeds and spores of aquatic plants (and some terrestrial plants), ostracod valves, and diatom frustules. Sediment samples collected for the study of chironomids, molluscs, aquatic plants, and ostracods were usually 5 cc in volume, measured by packing sediment into a bottle cap having a volume of 5 cc, but smaller samples (1 or 2 cc) were used when fossil remains were very abundant. Each sediment sample was washed through a #60 screen (openings 250 microns), which was found to retain all types of fossil remains of interest in the present study. Chironomus plumosus was also collected in a #35 screen (openings 500 microns). The residue was poured onto a white or light-colored plate on which a series of parallel lines about 1 cm apart had been drawn with a grease pencil. The water was allowed to evaporate, often with the aid of the low heat of a hotplate. The dish was then examined under a binocular dissecting microscope, using magnifications of 25x to 60x, and fossil remains were picked out with a wet paint brush having only a few bristles. The parallel lines on the plate ensured examination of the whole plate, since the space between each pair of lines was traversed in turn. The fossils were placed in plastic boxes, grouped into species (ostracods also grouped into several size classes), glued to the bottom of the box with gum tragacanth solution, and counted.

Identification of fossil remains was based mainly on descriptions and illustrations of organisms found in the literature, as well as on

comparison with reference collections of some organisms and on personal assistance given by several taxonomists, including R. C. Bright (seeds and molluscs), W. A. Watts (seeds), and F. M. Swain (ostracods). Graphs were drawn for cores 69-1, 69-2, 69-3, 69-4, 69-5, and C (Plates 6-11), indicating the numbers of fossil remains of all species of ostracods, molluscs, aquatic plants, and chironomids found in 5 cc of sediment at each level. The counts show the number of single valves of ostracods, the number of whole snails, the number of single clam shells, the number of head capsules of chironomids, and the number of single seeds and spores of plants.

A study of diatom stratigraphy was carried out in three Elk Lake cores — the 69-6 core, the frozen short core, and the shallow-water short core. Quantitative sediment samples, usually 1 cc in volume, were placed in glass beakers (usually 50 cc), and the beakers were filled to approximately one third of their volume with nitric acid. A pinch of potassium dichromate crystals was added to each sample, and the sample was stirred. The beakers were heated on low heat of a hotplate for about 2 hours, with addition of nitric acid as evaporation reduced its volume. The beakers were then filled with distilled water and allowed to stand for at least one day in order to allow diatom frustules to settle to the bottom. Each beaker was then decanted, leaving the diatom frustules and other siliceous remains, which formed a visible whitish layer on the bottom of the beaker. The beakers were refilled with distilled water and the above process repeated 3-4 times until the decantate was clear. The residue was then poured into vials and diluted until the concentration of diatoms was suitable for making slides with sufficient spacing of diatoms to permit counting (accomplished by trial and error).

Slides were made by placing 0.1 cc (usually) of the diatom solution on a cleaned coverslip (washing the coverslip with Liquinox seemed to reduce the surface tension of the drop and allowed it to spread out on the coverslip). The coverslips were left on a warm hotplate during the application of the drop and until the water had evaporated. Care was taken in this process to prevent clumping of diatoms, which makes counting difficult. Clumping seems to result from water currents within the drop if the heat is too great and from disturbance of the drop by movement of the coverslip. The coverslip with its dried diatom remains was then placed on a hotplate on high heat for about a half hour in order to drive out water that may still have been held within the frustules. A drop of Hyrax mounting medium was placed on a glass slide, the coverslip placed on the drop, and the slide placed on a hotplate on high heat for about 15 seconds. The coverslip was pressed down quite firmly with wooden sticks during hardening in order to squeeze out excess mounting medium.

The slides were then labelled and examined under oil immersion on a Nikon microscope having 10x oculars and 100x fluorite objectives. Diatoms were identified by comparison with descriptions and illustrations given in Hustedt (1930) and Patrick and Reimer (1966). Diatom counts of 200 valves were made for each sample in the 69-6 core and in the frozen short core, while counts of 400 valves were made for each countable sample of the shallow-water short core. Percentages of each species (or groups of species) were plotted on graphs for core 69-6 (Plate 12) and the frozen short core (Plate 14). A summary of the data obtained in the counting of the shallow-water short core is given in Table 14. Diatom concentration (number of diatom frustules/lcc of sediment) and absolute diatom influx (diatom frustules/cm²/year) were

also calculated for the 69-6 core and the frozen short core (Plates 12 and 14), for which rates of sedimentation could be calculated from the annual laminae, at least in portions of the cores.

Ecological Studies

In order to supplement the ecological information available in the literature, several types of studies were designed to determine the ecological relationships of several of the groups of aquatic organisms which have been studied stratigraphically in Elk Lake cores. Most of the ecological studies were carried out in Elk Lake during the summers of 1968 and 1969, but a study in Green Lake in southern Minnesota in the summer of 1969 also contributed interesting ecological information concerning ostracods and molluscs.

Five methods of study of the modern ecology of aquatic organisms were used:

1) Collection of living ostracods and molluscs in surface sediments

Samples of surface sediment were collected in Elk Lake on June 13 and June 15, 1969, at the location indicated in Table 7. The surface sediment was collected with an Ekman dredge without much disturbance. Since ostracods live mainly in the upper 1 cm of sediment, a spoon was used to skim off the surface sediment to approximately this depth. This surface sediment was placed in labelled plastic bags. In the laboratory, measured amounts of sediment (usually 15-75 cc) were washed through a #60 screen. The residue of each sample was poured onto a white or light-colored dish and examined under a binocular dissecting microscope at magnifications of 25x to 60x. Living ostracods and small molluscs were picked out with the aid of a paint brush, and large molluscs and seeds by hand. Living organisms could usually be distinguished

from dead ones by their movement, but the screening method of removing the organisms from the sediment seems to have been the cause of immobilization of many ostracods, probably because of entrance of air between their valves (Ward and Whipple, 1918). Sometimes, however, the "eye" could still be observed moving in immobile ostracods, which indicated life. The easiest method of distinguishing living ostracods from dead ones was by their coloration, only living (and recently living) ostracods having the distinctive coloration of the species. The color is usually contained in a thin membrane on the inner surface of the relatively transparent valves, and this membrane presumably disintegrates soon after the death of the ostracod, leaving only the transparent valves to be preserved in sediments.

The living ostracods and molluscs were placed in plastic boxes, separated into species, identified, glued to the bottom of the box with gum tragacanth, and counted. Graphs were drawn to indicate the numbers of living ostracods and molluscs of each species counted in 30 cc of surface sediment (Plates 4 and 5).

2) Collection of living ostracods and molluscs associated with aquatic plants

Ostracods and molluscs associated with aquatic plants were studied by examining samples collected by underwater bagging of large aquatic plants in Elk Lake. M. C. Whiteside used SCUBA to collect several such samples at depths indicated in Table 8 on June 25 and June 28, 1969. The large plastic bags, containing portions of aquatic plants and the water surrounding them, were transported to the laboratory and washed through a screen. The aquatic plants were identified, but no attempt was made to estimate the quantity of plant material in each

bag. The residues were examined as in the surface sediment studies, and counts were made of living ostracods and molluscs found in each sample. The numbers of each species found in each sample is indicated in Table 8 and Plate 4.

3) Collection of living ostracods and molluscs in open water

Live traps, designed to catch actively swimming organisms, were set up in the littoral zone of Elk Lake by M. C. Whiteside in the summer of 1969. The traps were set about 1 m above the sediment surface to prevent entrance of strictly bottom-dwelling organisms. Traps consisted of an inverted funnel with a collecting bottle containing water. It was assumed that only actively swimming organisms could move upward through the funnel and be caught in the collecting bottle. The organisms found in the traps, indicated in Table 11, are therefore assumed to have been living at the time they entered the traps, even though they were preserved in alcohol when the samples were studied.

4) Ecological inferences made on the basis of distributions of fossil remains of ostracods, chironomids, and molluscs in surface sediments

The distribution of fossil remains of some benthic ostracods, chironomids, and molluscs in Elk Lake seems to represent the distribution of living organisms of these species, since there is evidence that movement of fossil remains in some parts of the basin of Elk Lake may be negligible. This evidence will be discussed under the section concerning distribution of fossil remains. If this is true, the fossil distribution is very informative in indicating the ecology of some benthic species. Such a study is in some respects superior to a study of living organisms, since fossil remains are much more numerous than living organisms in a given quantity of sediment. As well, the fossil

distribution represents the average range of distribution of a species, which varies in living organisms on a seasonal basis, and probably also on a yearly basis.

5) Survey of aquatic macrophytes

Several studies of the aquatic macrophytes of Elk Lake were carried out at the northern end of the lake in the summers of 1968 and 1969. On July 9, 1968, a qualitative survey of aquatic plants was made at the northern end of the northwest-southeast transect. Aquatic macrophytes were quite easily observed and identified from a boat since the water of Elk Lake was relatively clear. The abundance of the various species of aquatic plants was noted at stations located at 10-m intervals along the transect from the shore to a distance of 120 m from the shore, where, under 440 cm of water, no aquatic plants were visible from the boat.

A quantitative survey of aquatic plants in Elk Lake was made in late July of 1968 in relatively shallow water at the northern end of the lake. Seven 15-m transects, parallel to the shore, were set up by ropes suspended above the water between poles erected in the sediment. The transects were spaced at 2-m intervals from the shore to a distance of 14 m from the shore. At 2-m intervals along each transect, a wire hoop of about 75-cm diameter, attached to a pole, was placed on the bottom sediment, and all plants occurring within the hoop were recorded, either as numbers of individuals of large aquatic plants, or as percentage cover of smaller mat-forming plants. An underwater telescope, consisting of a vertical metal cylinder with its lower end closed by glass, was used in some cases to view the underwater vegetation. The glass bottom was pushed beneath the surface of the water and

the vegetation viewed through the cylinder. The water depth at each sampling station was measured and recorded.

Some ecological information concerning the aquatic plants of Elk Lake was derived from the underwater sampling carried out by M. C. Whiteside in the summer of 1969 with the use of SCUBA. Although the main purpose of the sampling was to collect aquatic plants for a study of the cladocerans, ostracods, and molluscs associated with the plants, the record of the occurrence of aquatic-plant species was valuable in itself. The species identified and the depths of the sampling stations are indicated in Table 8.

Studies of Fossil Distribution in Surface Sediments

A study was designed to determine the effectiveness of water movement in redistributing fossil organisms after death. This study, carried out in Elk Lake in the summers of 1968 and 1969, was intended to supplement the scanty information on this subject available in the literature. The study yielded data concerning the distribution of fossil ostracods, molluscs, chironomids, seeds, and other fossil remains in the surface sediments of Elk Lake and, through a comparison between the distribution of fossil and living organisms, some suggestions concerning redistribution of fossils after death were made.

The distribution of fossil remains was determined by the study of surface-sediment samples collected by Ekman dredge in a transect from the northwest to the southeast end of Elk Lake. Samples collected for the study of seeds and other fairly large plant fragments were taken at the locations indicated in Figure 7. From each sample, 100 cc of sediment were washed through a #60 screen, and the residue was poured onto a white or light-colored dish and examined under a binocular

dissecting microscope at 25x to 60x magnifications. The fossils of interest to the study were picked out with a paint brush, placed in plastic boxes, and counted. The numbers of plant fossils found in each 100-cc sample are indicated in Figures 6-9 and Tables 5 and 6. In the same samples, fossil cladoceran ephippia and other small unidentified aquatic animal remains were identified, and the results of the counts are indicated in Table 6 and Figure 10. The locations of samples in which fossil ostracods, molluscs, and chironomids were studied are indicated in Plates 4 and 5. Sediment samples of 5 cc or 7 cc were washed through a #60 screen and studied as described above, except that residues were allowed to evaporate to dryness on the dish before the fossils were picked out with a wet paint brush. Graphs indicate the numbers of fossil remains of ostracods, molluscs, and chironomids in 5 cc of sediment (Plates 4 and 5). Species of ostracods, molluscs, and chironomids were grouped according to their patterns of distribution into several types of depth distribution. If fossil and living distributions are the same, one may assume that no redistribution of fossils by water movements is taking place. Discrepancies between fossil and living distributions of organisms suggest that some process is operating within the lake that transports after death.

STRATIGRAPHIC AND SUPPORTING STUDIES

PART 1 - POLLEN ANALYSIS

The vegetational history of the Itasca State Park region is already quite well understood through the detailed pollen studies of McAndrews (1966) on Bog D, located about 3 miles southeast of Elk Lake, Janssen (1967) on Stevens Pond, located just beyond the northern boundary of the park, and Shay (1971) on Nicollet Valley, located at the southern end of the south arm of Lake Itasca. The pollen analyses carried out in the present study on nine sediment cores from Elk Lake were intended to serve mainly as supporting studies in the paleolimnological investigations of Elk Lake. In this respect, the main purpose of the pollen studies were 1) to establish stratigraphic relationships among the several cores of Elk Lake, and 2) to correlate the paleolimnology of Elk Lake with the history of the terrestrial vegetation of the region. Because pollen analysis in the present study is subsidiary to the paleolimnological analyses and because the pollen diagrams are very similar to the Bog D diagram, the history of vegetation implied by the pollen analyses will be discussed only briefly and with emphasis on new information derived from the Elk Lake study. The pollen assemblage zones described have been delimited mainly on the basis of the key to pollen assemblage zones set up by McAndrews for the Bog D pollen diagram, and his nomenclature has been adopted for most of the zones.

The pollen of the basal clastic sediments found in cores C, 69-1, 69-2, 69-3, and 69-5 is of particular interest because it may record the vegetational changes taking place during a period of time not represented in the Bog D diagram, for Bog D was filled with a buried

ice block at this time. The vegetation for this period is rather difficult to interpret, for pollen counts include many poorly preserved pollen grains that may have been redeposited from older sediments. Some of these pollen grains may be of Cretaceous age, for some of them resemble the conifer pollen illustrated by Pierce (1961). On the pollen diagram of the 69-5 core, poorly preserved grains were distinguished from well-preserved grains only for the conifers, but a complete tabulation of well-preserved and poorly preserved grains was made on three samples, as shown in Table 1. Among the conifers, Quaternary Picea grains are quite easily distinguished from poorly preserved conifer grains by their excellent preservation and by their distinctive structure, but well-preserved Pinus grains closely resemble the poorly preserved conifer grains and are grouped together with them in the basal clastic sediments of the 69-5 and 69-2 pollen diagrams. However, Pinus is always represented by very low percentages in pollen counts of the spruce-dominated pollen zone in pollen diagrams in northern Minnesota (Wright, 1968). Therefore it is concluded that Quaternary Pinus pollen grains form a very small percentage of the counts in this combined category, and that most of the other grains are of Cretaceous origin.

Although the presence of poorly preserved pollen grains makes the interpretation of the pollen diagram within the basal clastic sediments rather difficult, it is possible to make some suggestions concerning probable vegetation changes within this time period. The following pollen zones may be recognized in the pollen diagram of the 69-5 core.

1. Herb pollen zone (?)

The lowest sample (1625 cm) analyzed in the 69-5 core seems to

| | | 1453cm | 1465cm | 1485cm |
|--------------------------------|----------------------------------|--------|--------|--------|
| Well-preserved pollen grains | <u>Pinus</u> ? | - | 7½ | 6½ |
| | <u>Picea</u> | 2½ | 10½ | 21½ |
| | <u>Larix</u> | - | - | 2 |
| | <u>Betula</u> | - | - | 1 |
| | <u>Salix</u> | 1 | 1 | 2 |
| | <u>Fraxinus nigra</u> | - | 2 | 3 |
| | <u>Quercus</u> | - | 1 | - |
| | Gramineae | - | - | 4 |
| | Cyperaceae | 3 | 2 | 1 |
| | <u>Artemisia</u> | 1 | 4 | 2 |
| | <u>Ambrosia</u> | - | 2 | 2 |
| | Tubuliflorae | 1 | - | 2 |
| | Chenopodiaceae- Amaranthaceae | - | 2 | - |
| | <u>Saxifraga</u> ? | 1 | 1 | - |
| Poorly preserved pollen grains | Undifferentiated conifer | 7 | 33 | 30 |
| | <u>Alnus</u> | 1 | - | - |
| | <u>Betula</u> | - | 1 | 1 |
| | <u>Corylus</u> | - | - | 1 |
| | <u>Ostrya</u> | 1 | 3 | 1 |
| | <u>Acer</u> | - | - | 1 |
| | Gramineae | - | 2 | - |
| | <u>Artemisia</u> | 2 | 4 | 2 |
| | <u>Ambrosia</u> | 1 | 3 | - |
| | Chenopodiaceae- Amaranthaceae | - | 1 | 1 |
| | <u>Typha</u> | - | 1 | - |
| | Indeterminate | - | 19 | 16 |
| | Total | 32½ | 100 | 100 |

Table 1. State of preservation of fossil pollen grains counted in three samples of the 69-5 core.

show relatively little poorly preserved pollen, so most of the pollen grains are probably contemporaneous. The high NAP (non-arboreal pollen) of this sample seems to place it in the herb pollen zone that has been identified in the early lateglacial period of several sites in Minnesota, including Weber Lake (Fries, 1962), Kotiranta Lake (Wright and Watts, 1969), Spider Creek (Baker, 1965), White Lily Lake (Cushing, 1967), Madelia (Jelgersma, 1962), and Glatsch Lake (Wright and Watts, 1969). The Compositae - Cyperaceae assemblage zone is defined by Cushing (1967) by a NAP percentage of 50% or higher. The high percentage values of Gramineae, Cyperaceae, and Artemisia in the Elk Lake sample is fairly typical of this assemblage. The pollen of Betula and Salix in this sample may represent local vegetation, but pollen of Alnus and Ostrya, if contemporaneous, probably represents far-travelled pollen grains from distant thermophilous vegetation, which is the usual interpretation of this characteristic feature of the herb pollen zone at all sites in Minnesota where the zone is represented (Wright, 1968). This dominance of non-arboreal pollen, as well as the very low absolute pollen frequency in the herb pollen zones of Minnesota, have led to the interpretation of this pollen assemblage as representative of a tundra vegetation, at least in northeastern Minnesota, where macrofossils of tundra plants have confirmed this interpretation (Wright, 1968).

Low absolute pollen frequency is indicated in this sample by very high counts of Ailanthus pollen, but this is not considered reliable evidence of low absolute pollen influx, for rate of sedimentation may have been very high. This is confirmed by the observation that even when local Picea trees were present, as indicated by Picea needles in cores C and 69-2, the absolute pollen frequency is very low in the basal clastic sediments. Thus the interpretation of the lowest pollen

sample in the 69-5 core as representing tundra vegetation is based only on the fairly high NAP, which, because of the possible contamination by redeposited pollen, is also unreliable.

2. Picea assemblage zone

All samples between 1625 cm and 1448 cm in core 69-5 exhibit a definite dominance of Picea pollen, which is well preserved and therefore considered to represent contemporaneous vegetation, and these samples therefore may be placed in the Picea assemblage zone, similar to the Picea-Populus assemblage zone described by McAndrews (1966). However, the lowest sample of this zone, 1575 cm (subzone a in Figure 3), although showing a very high Picea pollen percentage, does not contain pollen of the other typical components of the Picea forest, Abies balsamea, Larix laricina, and Fraxinus nigra. The Picea pollen in this sample may represent a spruce forest in which these species are absent, perhaps due to a lag in migration, or the Picea pollen may represent transported Picea pollen grains from the forest margin some distance away. Similar pollen percentages were found in the lowest sample (851 cm) of the 69-2 core. The pollen percentages of the upper part of the Picea zone in core 69-5 (subzone b in Figure 3), however, seem to represent local Picea forest, since pollen grains of the associated trees are present. Pollen of these species is also found in the uppermost samples of the clastic sediments of cores 69-2 (depth 845 cm) and C (1593 cm). Also, considerable numbers of Picea needles were found in the upper several centimeters of the clastic sediments in each of these two cores, suggesting either that Picea grew on the slopes of Elk Lake or that Picea needles were carried with the clastic materials from a nearby location.

3. Other assemblage zones

Above the Picea zone, pollen percentages of Elk Lake cores closely resemble those of the pollen diagram from Bog D and the interpretations of vegetation given by McAndrews on the basis of changes in pollen percentages have not been modified. In the Elk Lake pollen diagrams 69-5, 69-2 and C, there is evidence that the Picea forest continued for a short time after the organic lake sedimentation began, but in each diagram the Picea pollen percentage begins to decline immediately above the change in sediment (Fig. 3). In cores 69-2 and 69-5 Picea pollen dominance is replaced by Pinus pollen dominance within very few centimeters of sediment (about 2 cm in 69-2 and 2-12 cm in 69-5) which probably represents a relatively short period of time. However, in core C the Picea pollen percentage declines gradually in about 72 cm (from sediment boundary at 1592 cm to Pinus maximum at 1520 cm) of organic sediments above the sand. This is probably the result of a much higher sedimentation rate at this location during this period. Perhaps there was a depression in the basin at this location which permitted a considerably higher sedimentation rate. The great difference in the length of core represented by the Picea pollen zone within faunal unit B in the several Elk Lake cores (Plate 1) is the result of this difference in sedimentation rates during this period.

The six pollen samples analyzed in this 72-cm transition zone in core C seem to indicate a successional sequence from Picea to Pinus pollen maxima which suggests that, although climatic warming undoubtedly was the ultimate factor causing the succession to Pinus forests, the Picea forest may have been destroyed by fire. The marked decrease in Picea pollen is accompanied by an increase in pollen of the light-loving plants Juniperus? and Artemisia and in pollen of Populus,

ELK 69-2

ELK C

ELK 69-5

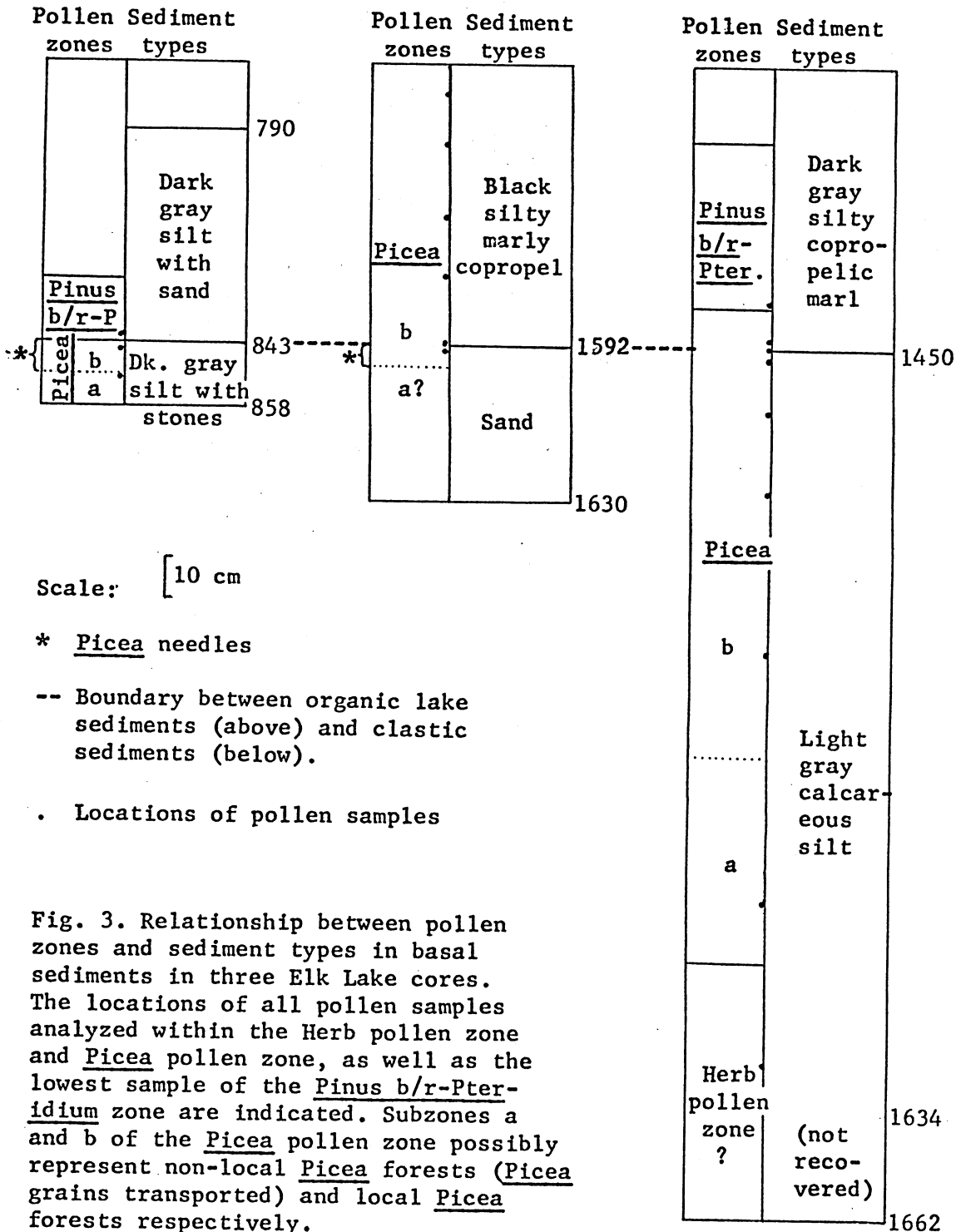


Fig. 3. Relationship between pollen zones and sediment types in basal sediments in three Elk Lake cores. The locations of all pollen samples analyzed within the Herb pollen zone and Picea pollen zone, as well as the lowest sample of the Pinus b/r-Pteridium zone are indicated. Subzones a and b of the Picea pollen zone possibly represent non-local Picea forests (Picea grains transported) and local Picea forests respectively.

which often invades after a fire. These pollen maxima are succeeded by a pollen maximum of Betula, a species that can replace Populus in secondary succession (Curtis, 1959), and finally by the Pinus pollen maximum. The Pinus banksiana/resinosa-Pteridium assemblage zone that follows is interpreted by McAndrews as representing open stands of Pinus banksiana trees with an understory of Pteridium.

The Pinus banksiana/resinosa-Pteridium assemblage zone is followed by the Quercus-Gramineae-Artemisia assemblage zone, as in Bog D. This assemblage zone, characterized by fairly high pollen percentages of Quercus as well as of several prairie herbs, is believed by McAndrews to represent an oak savanna, probably with Quercus macrocarpa as the most abundant oak. The Quercus-Ostrya assemblage zone, having relatively high pollen percentages of several deciduous trees, succeeds the Quercus-Gramineae-Artemisia zone. This pollen assemblage zone presumably represents a mesic deciduous forest containing Ostrya, Ulmus, Tilia, Fraxinus, and Acer saccharum. Finally, Pinus strobus migrated into the area and a Pinus strobus forest has dominated the vicinity of Elk Lake until the present.

The dates of the pollen-zone boundaries in Elk Lake may be estimated by comparison with nearby Bog D, which has a very similar sequence of pollen zones. Thus, deposition of the Pinus banksiana/resinosa-Pteridium assemblage zone began about 11,000 B.P., the Quercus-Gramineae-Artemisia assemblage zone about 8,500 B.P., the Quercus-Ostrya assemblage zone about 4,000 B.P., and the Pinus strobus assemblage zone about 2,000 B.P. However, the C^{14} dates obtained by Shay (1971) in the Nicollet Valley study are considerably younger. Since Shay's dates are based on C^{14} analysis of wood fragments in most cases, they are probably more

accurate than the dates of McAndrews which were based on C^{14} analysis of sediments probably containing a considerable amount of old carbon derived from weathering of sedimentary rocks. Shay's analyses date the beginning of the Pinus banksiana/resinosa-Pteridium zone at 9,500 B.P. and the beginning of the Quercus-Gramineae-Artemisia zone at 7,500 B.P.

PART 2 - SEDIMENT STRATIGRAPHY

Considerable information concerning past limnological conditions within a lake can be derived from a study of the physical and chemical characteristics of lake sediments in cores (Frey, 1964). In the present study of Elk Lake, some inferences concerning past water levels, productivity, and water-circulation patterns will be made on the basis of sediment characteristics alone, before consideration of fossils. The study of the general physical and chemical characteristics of several cores, with sediment stratigraphy correlated mainly by pollen analysis, has provided a horizontal profile of the sediments of Elk Lake (Plate 1). Since the boundaries between sediment zones indicated on the diagram prove to be time-parallel by comparison of pollen profiles, it is possible to determine the relationships between sediment types and rates of deposition in various parts of the basin in the same time periods. This general stratigraphic profile, as well as well as information derived from more detailed analyses of a few cores, has led to some interpretations of limnological events occurring in the lake in the past. Correlation of these events with the changes in terrestrial vegetation has been inferred from the pollen profiles.

1. Water level

Relatively little information pertaining to past water levels in Elk Lake can be derived from the examination of core sediments. Only one probable change in water level is indicated in the sediment stratigraphy of Elk Lake cores, but evidence for at least two other water-level changes in Elk Lake is found in other sources. Firstly, there was probably a lowering of water level during the time of the Quercus-Gramineae-Artemisia zone. Although no definite evidence of such a

change in water level is provided by Elk Lake sediment stratigraphy, this suggestion is made on the basis of the sediment stratigraphy of two other nearby water bodies. Nicollet Creek sediments show a gap in the sediment record from the middle Quercus-Gramineae-Artemisia period until the Pinus period (Shay, 1971). This suggests either that sedimentation ceased as a result of drying up of the creek bed in the middle Quercus-Gramineae-Artemisia zone or that sediments deposited in the period were subsequently removed by erosion. In Bog D, McAndrews (1966) recorded the occurrence of peaty gyttja and moss sediment in the Quercus-Gramineae-Artemisia zone, compared to pure gyttja in the rest of the core, possibly indicating a shallower water level in this period.

Evidence for a rise in water level, probably to the present level, in the middle of the Quercus-Ostrya zone is found in the Elk 69-1 core, in which sedimentation resumed at this time after a long gap, probably since the herb zone (only three pollen grains were found in the lower sediments). If sediment had been deposited at this location in an earlier period of high water, they must have been removed by erosion in a subsequent low-water-level period.

Finally, historical information indicates that a recent rise of water level of about 1 m has resulted from the construction of a dam across the outlet of Elk Lake at Chambers Creek during the logging operations carried out in the vicinity of Elk Lake early in this century, especially 1917-1919 (Dobie, 1959).

2. Productivity

Some inferences concerning productivity of a lake in the past can be made by determining the percentage of organic matter in the sediments, by calculating past rates of sediment accumulation, and by

observing color changes in the sediments. Deevey (1955) observed that in Linsley Pond and in Windermere the eutrophication of the lakes, interpreted mainly on the basis of changes in chironomid species, produced increases in both the percentage of organic matter in the sediments and in the rate of accumulation of the sediment. Therefore such information derived from Elk Lake cores will be presented, and possible interpretations concerning lake productivity will be proposed.

a) Percentages of organic matter

Determinations of organic matter were carried out for core 69-5 (Plate 2). The percent organic matter is very low (3-4%) in the lowest sediments, increases steadily through the upper Picea zone, remains fairly steady at about 8-10% through the Pinus, Quercus-Gramineae-Artemisia, and early Quercus-Ostrya zones, and increases in the upper Quercus-Ostrya zone, reaching about 16-18% in the upper Pinus strobus zone. This core analysis did not include the uppermost 10 cm of sediment, which presumably has a higher percent organic matter since the sediment is darker in color.

The interpretation of past lake productivity on the basis of organic-matter percentages of lake sediments faces several problems. Firstly, the percentage of organic matter in sediment depends not only on the amount of organic matter being deposited at a given time, but on the amount of other material (mineral, precipitated carbonate, etc.) being deposited at the same time. Another problem lies in the possibility that the amount of oxygen in water overlying sediments may determine whether the organic matter is preserved in the sediment (under conditions of low oxygen) or decomposed and released back into the lake in inorganic form under conditions of high oxygen (Ruttner, 1953).

The two periods of increasing percentage of organic matter in Elk

Lake cores must be discussed in the light of these possible problems. The first increase in organic matter, in the Picea zone, is probably related to an increase in productivity resulting from the warming of the climate at the time of the spruce fall, as a similar sediment change was interpreted in Weber Lake by Fries (1962). The increase in organic matter percentage which began in the middle Quercus-Ostrya zone seems also to reflect an increase in the productivity of Elk Lake, which is consistent with the fossil stratigraphy of Elk Lake cores. Eutrophication in Elk Lake at that time probably reflected an increase in nutrients in Elk Lake, which may have been related to the establishment of the Quercus-Ostrya forest in the watershed of the lake.

b) Sediment accumulation

i) Long cores

Approximate deposition times (yrs/cm), which are approximately the reciprocals of sedimentation rates, were calculated for some of the Elk Lake long cores by the methods described earlier. The values calculated for the 69-5, 69-2, and C cores may not be reliable since they are based on C^{14} dates of the Bog D core applied to corresponding pollen-zone boundaries in these Elk Lake cores. The deposition times calculated for the 69-6 core were based on the counting of laminae, and are therefore considered to be more reliable.

The interpretation of changes in deposition times in terms of past productivity of Elk Lake is hampered by the same problems as in the interpretation of organic-matter percentage, for deposition times depend not only on the deposition of organic matter but on the deposition of other materials as well, and some of the organic matter may

be decomposed under conditions of high oxygen and thus not be preserved in the sediments. Another problem is the possibility that changes in lake circulation may cause changes in deposition rates at a particular location in the lake. The very slow rate of sedimentation in the Quercus-Gramineae-Artemisia zone in the 69-5 core, located on the central ridge, may have resulted from the strong circulation of the lake in this Quercus savanna period in which other evidence (from the 69-6 core) indicates deeper and/or more frequent circulation than in later periods. Other problems involved in the interpretation of the deposition times includes the effect of compaction of sediment since deposition and the possibility of removal of sediment by erosion since deposition.

Despite these problems in interpretation, the considerably higher rate of sediment accumulation in the Quercus-Ostrya and Pinus strobus zones seems to confirm the possible increase in productivity of Elk Lake which began in the Quercus-Ostrya zone, as was suggested by the increasing organic matter percentage at this level. This increase in rate of sediment accumulation in the Quercus-Ostrya zone is found in the 69-5 core and also in the other cores in relatively shallow waters of Elk Lake, as indicated below in Table 2.

Table 2. Deposition times in several Elk Lake cores.

| | Early <u>Pinus b/r-Pteridium</u> to middle <u>Quercus-Ostrya</u> | Middle <u>Quercus-Ostrya</u> to present |
|------|---|--|
| 69-2 | 55.8 yrs/cm | 11.3 yrs/cm |
| C | 112.0 yrs/cm | 19.2 yrs/cm |
| 69-5 | 69.6 yrs/cm | 29.7 yrs/cm |

In contrast to the considerable changes in deposition times in

the relatively shallow-water cores, the deposition times seem to have changed very little in the deepest basin of Elk Lake since the Quercus-Gramineae-Artemisia zone. The average deposition times calculated by the counting and measuring of laminae in the Elk 69-6 core are indicated in Table 3.

Table 3. Deposition times of Elk Lake core 69-6, calculated on the basis of counting of laminae.

| | Depth of core segment(cm) | Portion of core segment laminated (%) | Average deposi- tion time (yrs/cm) | Number of laminae counted or calcu- lated in segments |
|------------------------------------|------------------------------|---|--|---|
| <u>Pinus strobus</u> | 2906-2956 | 100 | 3.6 | 180 |
| | 2956-3051 | 100 | 4.7 | 444 |
| | 3051-3147 | 100 | 5.2 | 500 |
| | 3147-3240 | 100 | 5.8 | 539 |
| | 3240-3337 | 100 | 5.6 | 547 |
| <u>Quercus-Ostrya</u> | 3337-3429 | 100 | 6.3 | 582 |
| | 3429-3485 | 100 | 5.9 | 333 |
| | 3485-3561 | 68 | 5.6 | 424 |
| | 3561-3658 | 42 | 4.4 | 427 |
| <u>Quercus-Gramineae-Artemisia</u> | 3658-3755 | 12 | 5.0 | 485 |
| | 3755-3855 | 23 | 4.7 | 456 |
| | 3855-3955 | 20 | 5.5(7.4 in 39cm) | 615 |
| | 3955-4055 | 15 | 5.9(8.8 in 29cm) | 662 |
| | 4055-4155 | 23 | 6.0 | 588 |
| | 4155-4255 | 33 | 7.8 | 780 |
| | 4255-4355 | 74 | 5.5 | <u>550</u> |
| | | | | 8112 |

The average deposition time before the middle of the Quercus-Ostrya zone cannot be determined by the approximate dating of pollen-zone boundaries, as in the shallow cores, since it is not possible to correlate the bottom of the core with a dated level in Bog D — the pollen percentages at the bottom of the core fit anywhere in the Quercus-Gramineae-Artemisia zone of Bog D. Neither can the deposition time be accurately determined by counting of laminae, for laminae are present only in small scattered portions of the core before the Quercus-Ostrya zone. But the average deposition time in this period, calculated on the basis of countable laminae, is about 5.6 yrs/cm. Two core segments contain zones of finer laminations (not included in the calculated average) which may represent drought periods in which the rate of sedimentation decreased because of lowered runoff to the lake. Four such zones were found, the lower 39 cm of the 3855-3955cm segment having a deposition time of 7.4 yrs/cm (representing about 290 years), and three small sections in the 3955-4055cm segment having an average deposition time of 8.8 yrs/cm.

The deposition time after the middle of the Quercus-Ostrya zone can be more easily calculated, for lamination is essentially continuous in the Quercus-Ostrya and Pinus strobus zones. The average deposition time calculated for this period is 5.6 yrs/cm, as in the lower portion of the core. The upper 50 cm of the core was not included in the calculation, for the apparently higher rate of sedimentation probably reflects the uncompacted nature of these sediments compared to lower sediments. The next segment below this seems also to exhibit a rate higher than normal for this zone, but the rate seems to reach a fairly constant value by 3051 cm (about 2 m below the sediment surface), suggesting that there is little further compaction of sediments

below this depth.

One might expect that the postulated increase in productivity midway through the Quercus-Ostrya zone would result in an increase in sedimentation rate. The productivity factor, however, may have been compensated by a change in lake circulation. During the time of the Quercus-Gramineae-Artemisia zone, the lake probably circulated quite vigorously under the influence of the strong winds that presumably prevailed in this dry period. The open savanna vegetation, which probably surrounded the lake, could provide little protection. The annual laminations of sediments in this zone are poorly developed, perhaps because of this greater water movement. Under conditions of greater circulation, more material could be transported into deep water, thus increasing the sedimentation rate there. These two opposing factors could thus account for sedimentation rates which were approximately the same before and after the postulated increase in productivity.

ii) Short cores

An abrupt increase in productivity in Elk Lake in recent times is suggested by a decrease in deposition time (presumably indicating an increase in sedimentation rate) in both short cores examined. In the shallow-water short core (SCs) taken at a water depth of 775 cm, a distinct darkening of sediments takes place at a depth of about 22 cm, suggesting increased content of organic matter in the upper sediments. This color change was observable in all of the cores taken from Elk Lake except the 69-1 and 69-2 cores, in which darkening is less conspicuous due to the abundance of light material being deposited, and in the deep-hole short core, in which sediments were already quite dark before the increase in productivity. The color change

in the shallow-water short core was accompanied by a considerable decrease in deposition time. The deposition time before the color change was calculated from the 69-4 core (taken from a nearby location) as 21.3 yrs/cm by dating the level at which Pinus pollen first reached high values in the Pinus strobus zone, through comparison with the dated Bog D pollen diagram. Above the color change, the average deposition time in the shallow-water short core was about 2.3 yrs/cm, representing an increase in sedimentation rate of almost 10 times.

The frozen short core (SCf) obtained from the deep hole of Elk Lake (Fig. 4) also suggests a considerable increase in sedimentation rate in recent times. At a depth of about 50 cm in the core, the narrow annual laminae typical of the upper part of the 69-6 core give way abruptly upward to a series of widely and irregularly spaced dark bands, which may represent thick lamination. (Since the top of the photographed frozen core was accidentally lost, the level at which the change in lamination took place was estimated from a more complete core taken in the winter of 1969.) The fine laminations just below the transition were being deposited at a rate of about 3.3 yrs/cm, while the average deposition time above the transition has been about 1 yr/cm, based on the date assigned to the transition by pollen analysis. The dark bands may be annual, but a distinct band was not laid down each year, since only 35 bands were counted, presumably representing a period of about 53 years (1917-1970 according to the interpretation of pollen profiles discussed below). (The bands were counted in the field by John Birks before the top of the core was lost.) The irregular spacing of bands in some portions of the core seems to support the supposition that bands were not formed in some years. The same problem

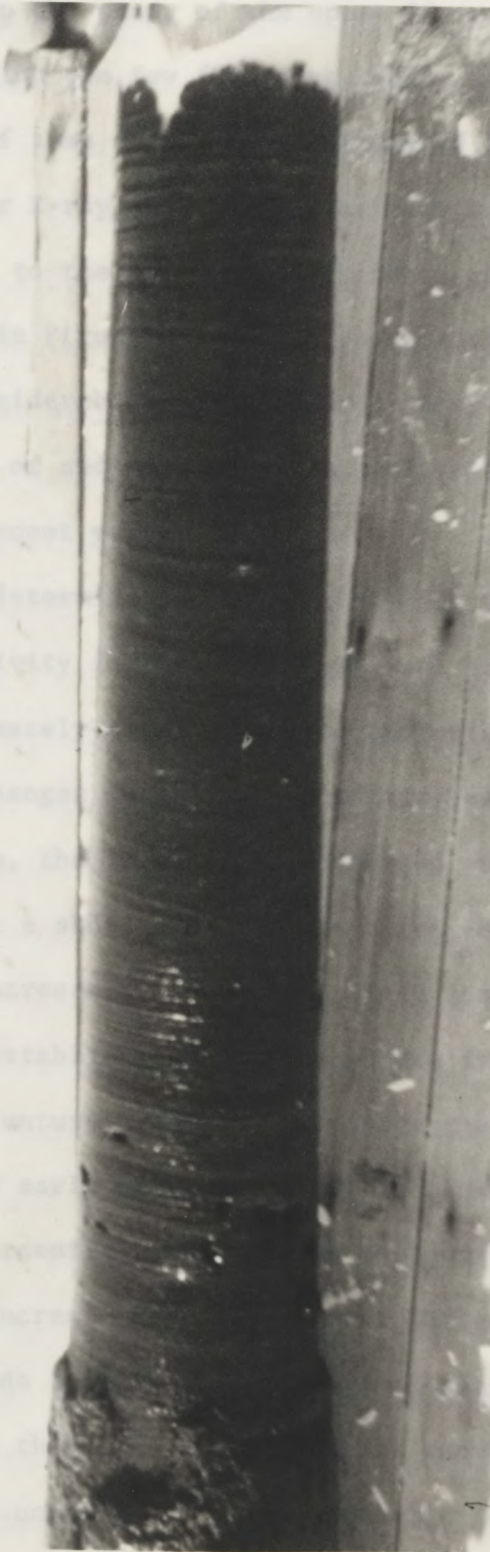


Fig. 4. Photograph of frozen short core

was encountered in the study of the upper 50 cm of the core from Lake Washington, in which too few (29) dark bands were recorded to represent the period of time supposedly represented by the sediment (52 years), even after X-ray analysis was carried out to detect possible bands not visible to the naked eye (Edmondson and Allison, 1970). The photograph shown in Figure 4 indicates also that the bands in the Elk Lake core are considerably closer together near the top, indicating a decreasing rate of sedimentation, probably reflecting a decrease in productivity in recent years.

In order to determine possible causes for the proposed recent increase in productivity in Elk Lake, the level at which the change took place was approximately dated by pollen analysis. In both short cores, two significant changes in pollen percentages provide a basis for dating. In both cores, the level of the proposed productivity increase was found to occur a short distance above the level at which Ambrosia pollen began to increase in percentage. This increase in Ambrosia pollen reflects the establishment of agriculture in northern Minnesota in the late 19th century and probably places the date of the productivity change in the early part of the 20th century. The marked decrease in Pinus pollen percentages observed in both cores at the level of the productivity increase provides an even better basis for dating. Dobie (1959) records that the main period of logging in Itasca State Park took place in the years 1917-1919. The heavy logging of Pinus trees at that time undoubtedly was responsible for the marked decrease in Pinus pollen percentages observed in both cores and establishes the date of the sediment change with a fair degree of certainty at about 1917.

The correlation and dating of the level of productivity increase

in the two short cores leads to speculation of possible causes of the abrupt change. Three sources of pollution at this time, all related to logging operations in the vicinity of Elk Lake, may be suggested. Firstly, a 1-m dam was built at the outlet of Elk Lake through Chambers Creek in order to facilitate the floating of logs from Elk Lake to Lake Itasca (Dobie, 1959). The increased productivity of Elk Lake may have resulted from the flooding of former shore areas and consequent fertilization of the lake with large quantities of soil. Secondly, the exposure of forest soils to erosion after logging may have been an important factor in increasing the productivity of Elk Lake. Janssen (1967) attributes the destruction of the mesotrophic bog forest and establishment of the eutrophic Typha latifolia mat in Stevens Pond to the increased inflow of nutrients into the pond by soil erosion following logging around the pond. Thirdly, Likens et al (1970) have attributed the greatly increased concentration of dissolved nutrients in streamwaters of a deforested area in Hubbard Brook Experimental Forest to the alteration of the nitrogen cycle in such a disturbed ecosystem. They state that "Whereas nitrogen is normally conserved in the undisturbed ecosystem, in the deforested ecosystem nitrate is rapidly flushed from the system in drainage water. The mobilization of nitrate from decaying organic matter, presumably by increased microbial nitrification, quantitatively accounted for the net increase in total cation-anion export from the deforested ecosystem." The result of this pollution of streams was the appearance of dense blooms of algae in Hubbard Brook each summer. It may be suggested that the proposed increase in productivity in Elk Lake was due, at least in part, to this factor. However, several conditions of the Hubbard Brook experiment make it quite different from

the Elk Lake watershed logging operation: (1) After cutting, no timber or other vegetation was removed from the watershed, whereas in most logging operations trees are removed and slash is often burned. It was the decay of this great quantity of cut vegetation that presumably produced the enrichment, according to the interpretation given by Likens et al. (2) Regrowth of vegetation was inhibited for two years by periodic application of herbicides. (3) Great care was taken to minimize erosion, and no roads were made on the watershed. The cover of dead vegetation would have also hindered soil erosion. In the Elk Lake watershed, soil erosion may have been considerably greater.

In each of the three possible sources of pollution discussed above, the effect may have been to cause an abrupt increase in lake productivity, followed by a gradual decrease in productivity as the watershed conditions reverted towards normal state. The abrupt beginning of the event is confirmed by the sharp transition in sediment characteristics in both cores, and the gradual reversion toward normal productivity conditions is indicated by the closer spacing of bands in the upper part of the core from the deep hole.

c) Sediment color

Sediment color was recorded for all of the cores in which the stratigraphy was described. The changes in color of Elk Lake sediments, which occur very abruptly in many of the cores, correspond very closely with the boundaries between the faunal units that have been delimited in the Elk Lake cores, as indicated in Table 4. The color changes may in some cases be related to productivity changes in Elk Lake. For example, the olive color of sediment of faunal unit E in almost all of the cores may be related to the increased productivity of this period

which is suggested by the fossil evidence.

Table 4. Sediment color of several Elk Lake cores.

| Faunal units | 69-5 | C | 69-2 and 69-3 | 69-4 |
|--------------|------------|-----------|---------------|-----------------|
| E | Olive | Olive | Olive | Olive |
| D | Gray | Dark Gray | Light Gray | incomplete core |
| C | Dark Gray | | Dark Gray | |
| B | | Black | | |
| A | Light Gray | Sand | Gravel | |

3. Water circulation patterns

Some indication of water movements within the Elk Lake basin in the past can be interpreted from the occurrence of shell zone deposits in cores 69-2, 69-3, 69-4, and SCs and from the study of laminae in cores 69-6.

a) Shell zone deposits

At the present time, Elk Lake exhibits a distinctive "shell zone" at a water depth of about 3 m. The "shell zone" consists of an accumulation of coarse materials such as mollusc shells, pieces of calcite that were probably precipitated on leaves of aquatic plants, as well as seeds, spores, and fragments of aquatic plants. The accumulation of shell zone deposits at this depth has probably been an important factor in the formation of the submerged bench that occurs around the periphery of Elk Lake. The shell zone is presumably formed by the transportation and deposition of coarse materials by wave-induced offshore bottom currents (Frey, 1964). The occurrence of mollusc shells

beyond the dense vegetation zone (shore to 1.5 m water depth) is here attributed to transportation by water currents, probably after death, rather than to the autumnal offshore migration and subsequent death of molluscs as suggested by Lundbeck (1926 and 1929 in Frey, 1964) and studied in Lake Itasca by Quade (personal communication). The inclusion of many different species of snails and clams, as well as other coarse materials in the deposits, suggests such passive transportation from the dense vegetation zone rather than migration.

Similar shell zone deposits occur in faunal unit E in cores 69-2, 69-3, and 69-4. Some features of water movements in Elk Lake may be suggested by comparing the stratigraphy of unit E deposits in these cores. The comparison suggests a strong influence of bottom topography on the effectiveness of water movements in carrying the fairly heavy shell zone materials. The depression that occurred at the location of the 69-2 core was probably filled first, levelling the bottom topography. The smooth and still fairly steep slope formed in this manner then made the currents very effective in carrying the coarse shell zone deposits to considerable depths as recorded in the 69-4 core, in which such deposits are found to a depth of 968 cm. The fairly large stones found in the 69-4 core at 960-965 cm probably were not carried from the shore, since no stones are found at comparable levels in Elk 69-2 and 69-3 cores. The stones were probably re-deposited from a nearby projecting exposure of till or outwash on the lake bottom. The irregularity of the bottom topography of the original lake bottom is demonstrated not only by the present bottom topography (Fig. 2) but also by the profile diagram of sediment stratigraphy (Plate 1).

During the deposition of the shell and marl materials in the 69-2 and 69-4 cores in the early part of unit E, very little sedimentation occurred in the Elk 69-3 core. About 5 cm of shell zone deposits were noted (708-713 cm) in the sediment examination of this core, but the fossil counts (Plate 8) did not include a sample in this section and therefore do not reveal the increase in shells. There may even have been some erosion of sediment at this location during this period since it was higher than the surrounding lake bottom, at least at the beginning of the period.

The difference in sedimentation rates in the lower part of unit E at the three locations represented by the cores 69-2, 69-3, and 69-4 is reflected in very different pollen diagrams in the three cores. During this period, vegetation was undergoing a change from Quercus-Ostrya to Pinus strobus forests. In the Elk 69-4 core, the transition from 15% to 76% Pinus pollen is represented by 25-60 cm of sediment and in 69-2 the transition from 16% to 72% Pinus pollen is represented by 50-110 cm of sediment, whereas in 69-3, the transition from 16% to 64% takes place in only about 10 cm of sediment.

At the end of the transitional period, when Pinus had reached high percentage values (pine peak in Plate 1), an abrupt change in the depositional regime of the lake occurred. Deposition of shells and other heavy shell-zone materials no longer occurred at the locations of the Elk 69-4 and 69-3 cores, but shell-zone deposition was limited to shallower water, being recorded only in the 69-2 core. This change in depth of the shell zone may represent a small increase in water depth, but the water depth had probably already reached approximately the modern level considerably earlier. The reason for the change may lie in the decrease in the steepness of slope of the

near-shore bottom caused by shell-zone deposits laid down in the transition period. Another possible explanation is an increase in the abundance of aquatic macrophytes at this time. Evidence for such an increase is found only in an increase in plant-inhabiting ostracods at this level in the 69-2 core, but no increase in Chara spores and Najas seeds is evident in this core until somewhat higher. Both of these factors, a decrease in slope and an increase in aquatic macrophytes, would probably decrease the strength and effectiveness of wave-induced currents transporting coarse materials, thus limiting the shell-zone deposition to shallower depths. Another possible cause of shallower shell-zone deposition in the Pinus strobus period is a possible decrease in the strength of waves, which may have resulted from protection of Elk Lake by the tall Pinus forests. Frey (1964) explains the formation of shell zones in lakes by stating that "in large lakes many mollusc shells, including those of fairly large unionids, tend to be moved offshore by wave-induced currents and turbulence to a definite zone at a depth approximating the wave base, where they accumulate." Since the depth to which wave activity is effective depends on the size of waves (Ruttner, 1953), larger waves have an influence at greater depths than smaller waves.

The occurrence of shell-zone deposits in the shallow-water short core (SCs) (Plate 13) is difficult to interpret. Shortly after agricultural settlement began (marked by the rise in Ambrosia pollen at 30-35 cm depth in this core), a marked change in the sediment characteristics of this core took place. The lower olive marly copropel gives way to a typical shell-zone sediment, which extends from 30 to 15 cm, with its maximum development at 22-28 cm. The graph indicating mollusc abundance during this period (Plate 13) demonstrates clearly the

occurrence of this shell-zone peak in the core. The gradual rise and decline in the numbers of fossil mollusc shells in this interval suggests a progressive change in lake conditions, but this may be misleading. The events responsible for the observed increase and decrease in shell-zone deposition may have produced abrupt changes, but subsequent mixing of fossil shells by turbulence at the sediment surface may have reduced the sharpness of the sediment boundaries. The presence of shell-zone deposits in the short core at a depth of 8 m below the present water level represents a dramatic change from pre-settlement conditions. Before this time (below 500 cm on 69-2 core, according to probable correlations with stratigraphy of the short core), marl and shells were being deposited at the location of the 69-2 core, which probably had a water depth of about 4 m (if water level before the dam was about one meter below the present level). There was no deposition of shell-zone materials at the location of the 69-3 core, which was then presumably at a water depth of about 6 m. But shortly after settlement, shell-zone deposits were laid down in water that was presumably 7 m deep. This represents a drop of 3-4 m in the depth of shell-zone deposition.

A lowering of water level may be advanced as a possible cause of the lowered shell-zone depth. In the shell-zone portion of the SCs core, occurrence of a few broken, apparently redeposited, shells of the early postglacial ostracod, Cytherissa lacustris, may suggest that lowered water levels exposed older deposits by erosion near the shore. But, although very rare, a few shells of this ostracod occur in sediments only 10 cm deeper in the core. Therefore, the shells deposited in the post-settlement period may represent animals living

in the lake. Historical evidence that water levels in Elk Lake were quite low in the period shortly after settlement has been recorded by Dobie (1959). Even though a dam had been built at the outlet of Elk Lake at the time of logging, "water to float the logs from Elk Lake to Itasca was so scarce that the lumbermen attempted to blow up beaver dams to secure an adequate supply". Dobie also relates that "sometimes the water was so low the logs had to be towed between the lakes by using horses and log hooks". One factor that may have had some effect on the water level of Elk Lake was the clearing of Chambers Creek for boats in 1908 (Dobie, 1959). No absolute depths were given, but the water level was probably not low enough to cause the 3-4 m drop in the shell zone as indicated in the core.

b) Study of lamination in core 69-6

The laminae of the 69-6 core provide some information concerning the probably circulation patterns of Elk Lake in the past. As discussed above, laminae are present only in scattered portions of the core below the Quercus-Ostrya zone but are continuous in the upper part of the core. This suggests that during the Quercus-Gramineae-Artemisia zone the lake experienced vigorous circulation, not allowing laminae to form even in deep water where this core was taken, while in later periods circulation was less vigorous. In order to investigate the probable circulation pattern of Elk Lake in the Quercus-Gramineae-Artemisia zone, the circulation of Green Lake in Kandiyohi County was examined. The lake is located near the western border of the deciduous forest in southern Minnesota and is thus assumed to represent a climatic and vegetational situation somewhat similar to that of Elk Lake in the Quercus-Gramineae-Artemisia

period. The lake was found to be completely circulating to a depth of 25 m under the influence of strong winds when visited on June 24, 1969. Under the same weather conditions the next day, Elk Lake, which is surrounded by towering pine trees, had a sharp thermocline at 7 m. The circulation pattern of Green Lake, however, may not represent conditions in Elk Lake during the Quercus-Gramineae-Artemisia period, because it is about twice as large as Elk Lake, and the size of a lake has a considerable influence on its circulation pattern through its effect on wind fetch.

PART 3 - AQUATIC ORGANISMS

Several groups of aquatic organisms were examined in the present paleolimnological study of Elk Lake, in line with the recent trend in paleolimnology toward such a "complex" approach. Russian paleolimnologists have for some time followed this approach, identifying all plant and animal remains in the sediments as closely as possible (Frey, 1964). This kind of study provides a much more reliable basis for the interpretation of past ecological conditions than the study of only one type of organism, especially when the interpretations based on each group of aquatic organisms are largely conformable with one another and with the interpretations of palynology (Frey, 1964). Chironomids, molluscs, aquatic plants, ostracods, and diatoms have been considered in the present study. Each group will be discussed separately. The taxonomy, ecology, modern distribution of fossils in the Elk Lake basin, and the stratigraphy in the Elk Lake cores will be considered in the discussion of each group of organisms.

The present study has not only considered several different groups of organisms but has produced a quantitative stratigraphy of the individual species, which has not been attempted by paleolimnologists until the recent study of Klassen et al (1967) in southwestern Manitoba. Russian paleolimnologists have adopted a quantitative approach in their studies, listing fossils as total numbers per unit volume of fresh sediment as in the present study. But some Russian authors made no attempt to identify the species present, some listed only dominant species, and some mentioned the species present at each level but did not break down the stratum totals according to the component species (Frey, 1964). In the present study, a quantitative

stratigraphy of individual taxa (species or genera in most cases) has been produced for each group of organisms studied stratigraphically. Graphs of the stratigraphy of fossils of aquatic organisms in Elk Lake cores are shown in Plates 6-14.

The faunal stratigraphy for the long cores may be described as two facies, viz. the deep-water facies (cores 69-5, 69-6, and C) and the shallow-water facies (cores 69-1, 69-2, 69-3, and 69-4). Within each facies the faunal units are considered to represent synchronous assemblages. In the absence of multiple radiocarbon dates, the two facies are correlated with one another by pollen analysis, which provides clear time-stratigraphic markers throughout the basin, because the pollen types used represent the regional upland vegetation. Because the faunal units established for the deep-water cores have a one-to-one correlation with those of the shallow-water cores on the basis of pollen stratigraphy, the same letter designations for faunal units (A-E) are used for both facies.

The faunal units were first established in the deep-water 69-5 core, on the basis of distinct changes in the stratigraphy of ostracods, chironomids, and molluscs. For the deep-water C core the C/D and D/E boundaries were established on the same basis, but the A/B and B/C boundaries were made by correlation of pollen zones between this core and the 69-5 core.

For the shallow-water cores, faunal units were first identified in core 69-2, except the B/C boundary, which was interpolated on the basis of pollen zonation. For core 69-3, which was taken only 22 m away from 69-2, faunal units A, B, and C can be easily identified, but the D/E boundary is placed at a lithologic change similar to that in the 69-2 core. For cores 69-1 and 69-4, pollen

stratigraphy was used to place the faunal zone boundaries.

The close correlation of the faunal units between the two facies suggests that the limnological changes that caused population changes in aquatic organisms affected shallow-water and deep-water communities simultaneously. The A/B boundary coincides with the beginning of the Picea pollen decline. It should be noted that unit A is identified in cores 69-2, 69-3 and C by pollen correlation because aquatic fossils are absent. The B/C boundary coincides with the boundary between the Pinus banksiana/resinosa-Pteridium pollen zone and the Quercus-Gramineae-Artemisia pollen zone. However, the C/D and D/E unit boundaries occur within a pollen zone rather than at a boundary and are thus more difficult to correlate from core to core.

Within each faunal unit, the fossils found in the shallow-water cores and in the deep-water cores are commonly different in species composition and abundance. Thus the shallow-water and deep-water cores are considered separately in the discussion of each faunal unit.

CHIRONOMIDS

1. Taxonomy

Chironomids represent a family (family Chironomidae) within the order Diptera of the class Insecta. Morphologically, the larvae of this family are distinguished from other fly larvae by the double fleshy prolegs under the thorax and at the rear (Needham and Lloyd, 1916). Many members of this family are also distinctive in their red color (hence the name "blood worms"), which is due to the pigment erythrocyanin, a hemoglobin compound that allows the animals to live in waters low in oxygen (Pennak, 1953).

The identification of chironomid remains in the Elk Lake study is based on the structure of fossil head capsules of larvae. The head capsules were identified by comparison with diagrams and descriptions included in papers by Stahl (1959) and Curry (1962). The following chironomids were identified: (* indicates identification based on Curry, 1962)

| | |
|--------------------------------------|-------------------------|
| <u>*Chironomus plumosus</u> Linnaeus | <u>Procladius</u> |
| <u>Chironomus</u> sp. | <u>Sergentia</u> |
| <u>Cryptochironomus</u> | <u>Stictochironomus</u> |
| <u>Endochironomus</u> | <u>Tanytarsus</u> |
| <u>Glyptotendipes</u> | |
| <u>*Harnischia</u> | |
| <u>Microtendipes</u> | |
| Orthocladiinae | |
| <u>Paratendipes</u> | |
| <u>Pentaneura</u> | |
| <u>Polypedilum</u> | |

2. Ecology

The main ecological factors determining the depth distribution of chironomid larvae in a lake seem to be sediment type and oxygen tension of the water. Chironomid larvae are most numerous on soft organic sediments, where many species fashion dwelling tubes out of bits of sediment cemented together by a secretion of their silk glands (Needham and Lloyd, 1916). These soft, flocculent tubes are built on bottom mud or are attached to solid supports such as stems or stones. Soft organic sediments also provide organic detritus, which is one of the principal foods of the filter-feeding larvae (Pennak, 1953). Chironomid larvae differ considerably in their oxygen tolerances, some requiring quite high concentrations of dissolved oxygen in water, and others able to withstand very low oxygen tensions. The different oxygen preferences of chironomid species has led to their use as indicators of lake types with respect to oxygen content. The modern German classification as presented by Lundbeck (in Deevey, 1941) recognizes three basic lake types - oligotrophic lakes (high oxygen) characterized by Orthocladius and Tanytarsus, mesotrophic lakes (medium oxygen) characterized by Stictochironomus and Sergentia, and eutrophic lakes (low oxygen) characterized often by Chironomus plumosus.

The ecology of living chironomid larvae has not been investigated in the present study of Elk Lake, but Cole and Underhill (1965) have studied the sublittoral and profundal chironomid larvae of Lake Itasca. Chironomus plumosus was found to be the most abundant chironomid species in the deeper water of the lake. A peak in abundance of this species occurs at a depth of 7 m in Lake Itasca, which corresponds to the boundary between the sublittoral and profundal zones (Fig. 5). Such a lower sublittoral-upper profundal summer maximum in benthic

fauna has been recorded by many other biologists, including Eggleton (1931) and Deevey (1941). These workers collected a seasonal series of samples to elucidate the method and cause of the formation of such a concentration zone, but a completely satisfactory explanation has not been found. Larvae occur at all depths in the spring, but as summer stratification proceeds, populations decrease in shallow areas and often completely disappear in deep zones, thus producing the typical concentration at the boundary of the lower sublittoral and upper profundal zones. The decline in population in deep waters may be the result of migration (Deevey, 1941) or of death of larvae (Underhill and Cole, 1967) as oxygen decreases. The population decline in shallow waters during the summer is also incompletely understood, but Underhill and Cole (1967) suggest that fish predation may be an important factor.

The depth distribution of living chironomid species in Elk Lake can probably be determined with considerable accuracy by the study of fossil head capsules in surface sediments which has been carried out in Elk Lake. There seems to be little transport of head capsules within the lake, since the depth distribution of fossil head capsules corresponds quite well with the depth distribution of living chironomids which would be expected in the lake on the basis of a knowledge of the ecology of Elk Lake species gained from other sources. This is demonstrated in Fig. 5, in which the depth distribution of fossil head capsules of Chironomus plumosus in Elk Lake is compared with the depth distribution of living animals of the same species in Lake Itasca. In both lakes, the maximum population numbers of this species occurs a short distance below the level of rapid oxygen decline (which corresponds closely to the thermocline in these lakes). (The level of rapid oxygen decline in 1967, which occurs at about 8-10 m as indicated in

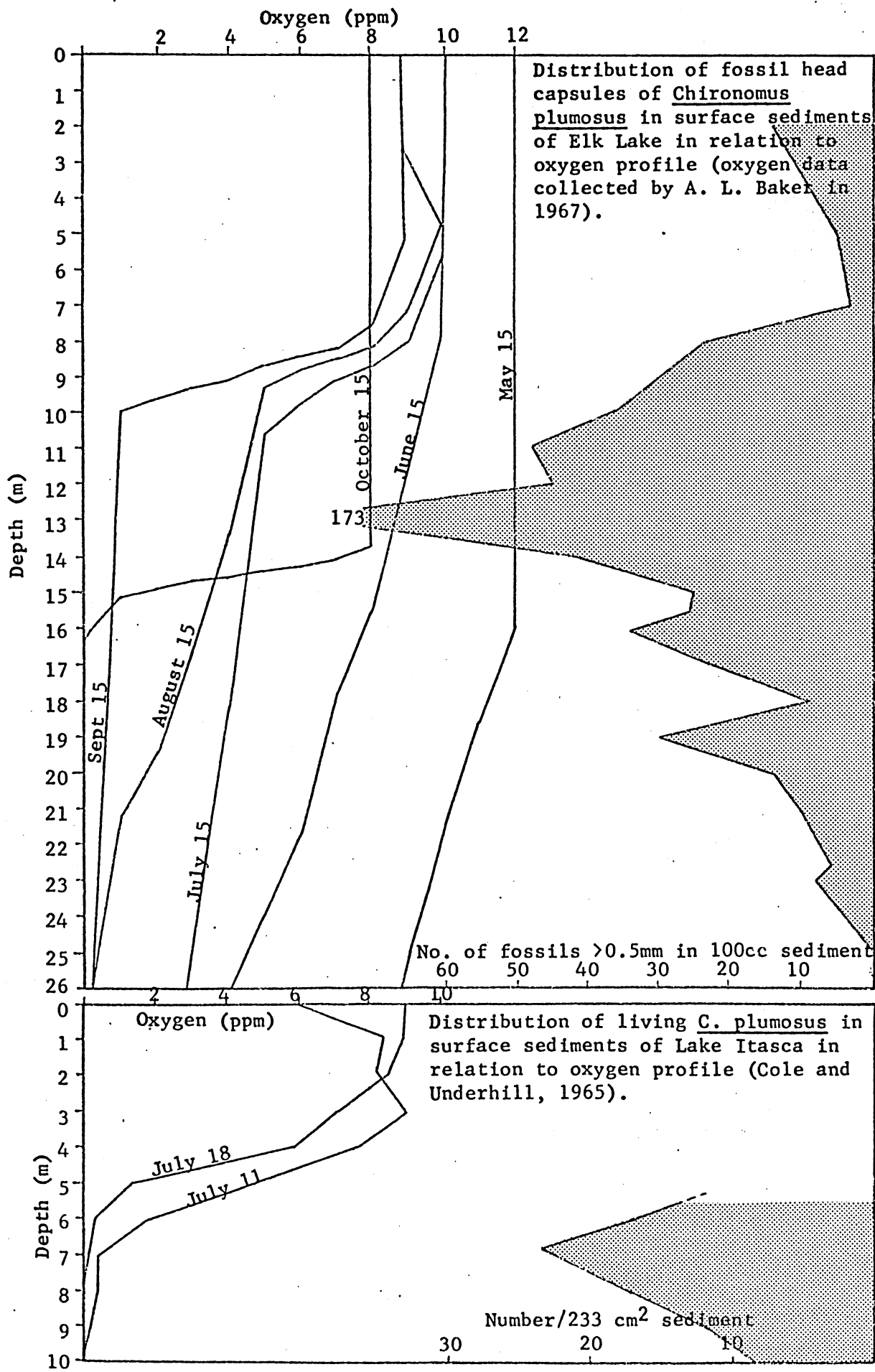


Fig. 5. Depth distribution of *Chironomus plumosus* in Elk Lake and in Lake Itasca.

Fig. 5, seems to represent the normal summer oxygen stratification of Elk Lake, according to the comparison between July oxygen profiles of 1965, 1966, and 1967 shown in Fig. 11.) This strongly suggests that the distribution of fossil head capsules of this species in Elk Lake represents the depth distribution of living animals.

As in the case of Chironomus plumosus, there is evidence that the fossil distributions of the rest of the chironomid species of Elk Lake also represent living distributions. The literature indicates that most of the species found near the shore in the study of fossil distributions (Plate 5) are forms that require high oxygen and thus would be expected to be living in this situation, i.e., Polypedilum (Miyadi, 1932-33), Endochironomus (Lindeman, 1942b), and Tanytarsus (Miyadi, 1930-31). However, Procladius, which is found in high numbers of fossils near the shore, is often reported as a deep-water species (Lindeman, 1942b; Eggleton, 1931; Underhill and Cole, 1965). The concentration of living shallow-water chironomids at a depth of about 5-6 m (Plate 5) would also be expected, for the soft sediments at this depth are the most favorable for chironomids, whereas low populations would be expected on the sand and coarse shell zone deposits closer to the shore.

3. Distribution of fossils in surface sediments

Little information is available concerning the extent of redistribution of fossil remains of chironomids in lakes, but Frey (1964) states that "since chironomid species usually have limited depth ranges in lakes, it is important in paleolimnological interpretations to know to what extent the exuviae and head capsules of littoral midges are transported offshore where they become incorporated

secondarily into deepwater sediments". The studies of Stahl (1959) have indicated that offshore transport of chironomid fossils may be relatively unimportant. The close correspondence between depth distribution of fossil chironomids and the expected depth distribution of living animals in Elk Lake, which was discussed above, is considered to be good evidence that relatively little transport of chironomid head capsules takes place in Elk Lake.

Two types of depth distribution of chironomids are indicated in Plate 5:

1) Chironomus plumosus assemblage: Only Chironomus plumosus is included in this depth-distribution category. Fossil head capsules are concentrated at all three points on the transect where the water depth is approximately 13 m and in a narrow maximum zone at about 6 m water depth at the northern end of the lake.

2) Endochironomus assemblage: Besides Endochironomus, this depth-distribution category includes Chironomus sp., Procladius, Pentaneura, Tanytarsus, Glyptotendipes, Polypedilum, Cryptochironomus, Orthocladiinae, Harnischia, Microtendipes, and Stictochironomus. Fossil head capsules of these chironomids are concentrated in relatively shallow water, commonly with a maximum at 5-6 m water depth at the southern end of the lake.

4. Stratigraphy

Several stratigraphic studies of chironomid head capsules have been carried out since the first such work was published in 1927 (Frey, 1964). An example of the typical midge succession in lakes is that of Linsley Pond, studied by Deevey in 1942, in which Tanytarsus dominated in the early oligotrophic phase of the lake,

followed by mesotrophic Endochironomus and Glyptotendipes, and then by eutrophic Chironomus (Frey, 1964).

Chironomid stratigraphy of the Elk Lake cores will be discussed with respect to the faunal units recognized in the lake:

Unit A - This unit is represented by chironomid fossils only in the 69-5 core. Very few fossils were found, the dominant genus being Procladius, with smaller numbers of Chironomus plumosus, Cryptochironomus, Microtendipes, Pentaneura, Stictochironomus, Tanytarsus, and two unidentified members of the family Orthocladiinae. The discrepancy in the interpretation of the ecology of Procladius was discussed earlier, and relatively little information is available concerning the ecology of the other genera represented. Little can be said, therefore, about the limnological conditions of this period on the basis of chironomid fossils except that the chironomid population is very different from that in succeeding units, and that the change in chironomid population from this unit to the following unit was very abrupt. The silt substrate may have been an important factor limiting and determining chironomid populations during this period.

Unit B - No chironomid fossils were found in this unit in the 69-2 core, probably because of the sandiness of the sediments. In the 69-3 core, in which a dark gray silt occurs, only three head capsules were found in this unit. In the cores from deep water, 69-5 and C, chironomids are well represented in this unit and have a similar assemblage: abundant fossils of Tanytarsus and Sergentia, small numbers of Chironomus plumosus, and very few Procladius. In core C, a few fossils of Microtendipes and Pentaneura were also found. The

high numbers of Tanytarsus and Sergentia in this unit suggest that there was considerable oxygen in the bottom waters at this depth in Elk Lake in this period, since both of these genera, Tanytarsus in particular, are known to require high oxygen conditions, as discussed above.

Unit C - In the nearshore cores 69-2 and 69-3, Chironomus plumosus enters the stratigraphy and is the dominant chironomid species, although total chironomid populations are low, probably due to the silt and sand substrate of this period. A few fossils of Procladius and some other types are also represented in this unit in the 69-3 core. In the deeper cores, 69-5 and C, the high populations of Tanytarsus and Sergentia of unit B decline abruptly to zero, being replaced by a moderate population of Chironomus plumosus, with very low numbers of Procladius and Pentaneura. Since Chironomus plumosus is a typical eutrophic chironomid species, lowered oxygen conditions in Elk Lake are suggested by this change in chironomid populations.

Unit D - In the nearshore cores 69-2 and 69-3, the chironomid populations show little change from the preceding period - low numbers of Chironomus plumosus fossils, with a few fossils of other types. There is also little change in the chironomid populations in the deeper cores, 69-5 and C, with moderate numbers of fossils of Chironomus plumosus.

Unit E - In the nearshore cores 69-2 and 69-3, the chironomid populations show little change from the preceding period, with low numbers of many species. Core 69-4 has the same assemblage, with increase in chironomid populations in the upper part of this unit,

probably because of the change in sediment from shelly copropel in the lower part to copropel in the upper part. In the deeper water cores 69-5 and C, there are generally higher numbers of Chironomus plumosus than in unit D, suggesting lowering of the oxygen content of the lake water. Other chironomid types are represented in smaller numbers.

Unit E' - This unit is delimited most clearly in the shallow-water short core (Plate 13), in which chironomid populations show a marked increase, suggesting a lowering of oxygen content of the lake waters and/or increasing productivity of the lake and/or more favorable sediment conditions for chironomid growth. The predominance of Chironomus plumosus and Procladius, both supposedly reflecting low oxygen conditions, supports the first suggestion. It may also be noted that both of these species exhibit their highest population numbers in the lower part of the unit. This seems to confirm the suggestion made above, based on width of laminae in the frozen short core, that the lake has been reverting towards normal conditions after a temporary disturbance, presumably the inwash of soil at the time of the building of the dam in 1917. The chironomid populations are still somewhat greater than before the disturbance, suggesting that the lake has not returned completely to pre-disturbance conditions. Although the population changes in Chironomus plumosus suggest changing oxygen conditions, the increase in other chironomids as well suggests an overall increase in lake productivity or the influence of more favorable sediment, for the sediments of this core change at the beginning of unit E' from an olive marly copropel to a dark marly copropel.

MOLLUSCS

1. Taxonomy

The phylum Mollusca is characterized by the ventral muscular foot, dorsal visceral hump and mantle (Beck and Braithwaite, 1962). Two classes of this phylum are represented in Elk Lake, the class Gastropoda (snails) and the class Pelecypoda (clams).

The identification of molluscs in the Elk Lake study has been based on the shape of shells in both living and fossil molluscs. The shells have been identified by the use of keys and diagrams (Baker, 1928; Eddy and Hodson, 1964) and by comparison with a collection of shells in the Bell Museum of Natural History, with the assistance of R. C. Bright. The following molluscs were identified in the Elk Lake study:

Amnicola limosa (Say)

Pisidium spp.

Armiger crista (Linn)

Promenetus exacuus (Say)

Ferrisia spp.

Sphaerium sp.

Gyraulus parvus (Say)

Valvata tricarinata (Say)

Helisoma spp.

Marstonia lustrica Pilsbry

Physa spp.

2. Ecology

The main ecological factors that affect the local distribution of molluscs are water chemistry, oxygen content of water, physical character of the substrate, and availability of food (Pennak, 1953). Calcium carbonate is essential for shell construction, so hard waters generally contain more species and individuals than soft waters

(Pennak, 1953). Most gastropods are limited to waters of high oxygen content (Pennak, 1953), but some pelecypods, especially Pisidium, are typical members of the profundal fauna (Eggleson, 1931; Juday, 1908 in Lindeman, 1942a). The physical character of the substrate is an important factor in the distribution of pelecypods and bottom-dwelling gastropods. Since many gastropods feed largely on the coating of living algae on aquatic macrophytes, they are most abundant on the stems and leaves of aquatic plants (Pennak, 1953). Amnicola limosa, Marstonia lustrica, and Gyraulus parvus are recorded as usual inhabitants of vegetation by Baker (1928). Most gastropods are restricted to shallow water, usually less than 3 m deep, where rooted plants are abundant.

A study of the living molluscs of Elk Lake and Green Lake was carried out as a part of the supporting studies in the paleolimnological investigation of Elk Lake. The numbers of living molluscs found in samples of surface sediments collected in a transect at the northern end of Elk Lake are shown in Table 7, and the numbers of living molluscs counted in the bagged plant samples are indicated in Table 8. Data obtained from surface sediment samples of Green Lake is shown in Table 10. Eight types of molluscs were collected - six snails and two clams. Several suggestions concerning the distribution of molluscs in Elk Lake and Green Lake may be made on the basis of these data:

- 1) Few molluscs besides Pisidium are found below a depth of about 4 m in both lakes, suggesting that most molluscs are essentially limited to the littoral zone in these lakes, probably associated with aquatic vegetation. Pisidium was found living in sediments

to a depth of 6 m in Elk Lake and 23½ m in Green Lake. The high oxygen content of Green Lake waters permits this clam to live at considerable depths, whereas in Elk Lake its depth distribution may be limited by the low oxygen content of deep waters. The literature cited above, however, records that Pisidium may occur in profundal zones of lakes, and it may be suggested that it actually lives at greater depths in Elk Lake than is indicated in the limited sampling study.

2) Comparison of data obtained from sediment samples in Elk Lake (Table 7) and that obtained from plant bag samples (Table 8) suggests that in Elk Lake some molluscs live both on aquatic plants and on bottom sediments, while others are restricted to bottom sediments. Amnicola limosa, Gyraulus parvus, Physa sp., and Valvata tricarinata were found in considerable abundance in both situations, while Pisidium, Sphaerium, Marstonia lustrica, and Ferrisia were found only on sediments. Sediment is the normal habitat of the clams Pisidium and Sphaerium, and Ferrisia is often found on rocks, dead naiad shells, and debris (Baker, 1928), but the apparent restriction of Marstonia lustrica to bottom sediments is not in accord with the ecological description of this species given by Baker (1928), who states that this species is "usually an inhabitant of vegetation and is particularly abundant in filamentous algae". However, other habitats cited by the same author were "sand" and "sand and gravel", which also seems to be the preferred habitat of this species in Elk Lake, as suggested by its distribution in surface sediments, most individuals being found in the nearshore sand samples.

3) Most molluscs living on the sediments seem to show a

preference for coarse sediments. Considerable numbers of living molluscs were found in the sand near the shore and in the coarse marly shell zone deposits (2-3.7 m), while no molluscs were collected in the soft black sediments at 1.4 m, and few in the black gyttja beyond the shell zone. Pisidium, however, seems to live equally well in the coarse sediments and in the soft black sediments beyond the shell zone. This genus is a member of the family Sphaeriidae, which is found on all types of bottom except clay and sand, unlike most pelecypods, which are restricted to stable sand and gravel substrates (Pennak, 1953).

3. Distribution of fossils in surface sediments

Considerable attention has been given to the distribution of fossil mollusc shells in lakes and the limnological phenomena involved in their distribution (Frey, 1964). Mollusc shells tend to be moved offshore by wave-induced currents and turbulence to a definite zone at a depth approximating the wave base, producing a typical "shell zone". Frey emphasizes that interpretations of shell deposits in sediment cores must take into consideration this common limnological process, which results in an accumulation of shells in a location where the animals did not live, and having a species composition quite unrelated to the populations that produced the shells. Another factor that determines the distribution of fossil mollusc shells in lakes is the dissolution of these calcareous shells under the acid conditions that often exist in the hypolimnion of lakes.

The distribution of fossil molluscs in Elk Lake (Plate 5) indicates the presence of a distinct shell zone. Shells of most species

of molluscs show a strong maximum in the 3.3 m sample at the northern end of the lake, and at 10 m at the southern end of the lake. The deeper shell zone at the southern end of the lake may be the result of stronger wave action and hence a deeper wave base, or it may reflect the more steeply sloping bottom topography which allows the offshore currents to carry molluscs to greater depths. Very few molluscs shells were found beyond the shell zones of Elk Lake, presumably because water currents were unable to carry the shells farther. The dissolution of mollusc shells probably has little importance in the limitation of fossil molluscs to relatively shallow depths in Elk Lake, for ostracod shells, many of which also contain considerable amounts of calcium carbonate, are well preserved at greater depths. Well-preserved fragments of mollusc shells were also found at considerable depths.

Three assemblages of fossil molluscs were recognized in the surface sediments of Elk Lake (Plate 5):

1) Gyraulus assemblage: This category includes Gyraulus parvus and Promenetus exacuus. Shells of these species are found in most samples in the littoral zone, with little evidence of a strong concentration in the shell zone.

2) Amnicola assemblage: This category includes Amnicola limosa, Marstonia lustrica, Physa spp., Valvata tricarinata, Ferrisia spp., Helisoma spp., and Sphaerium sp. Shells of these species show the typical shell zone pattern of distribution described above.

3) Pisidium assemblage: This category includes only Pisidium. Shells of Pisidium spp. seem to exhibit two zones of concentration, a strong maximum close to the shore and a smaller concentration at

the 3.3 m depth. This relatively heavy clam, which lives in the sediment, would not be expected to be transported by water currents as readily as the lighter snails, many of which live on aquatic plants. The distribution of this fossil clam therefore corresponds more closely to the distribution of its living forms, as indicated in Plate 5 and Table 7.

4. Stratigraphy

Many stratigraphic studies of mollusc fossils have been carried out, attempting to interpret the occurrence and changing abundance of mollusc species in terms of their present ecology. Mollusc stratigraphy has been interpreted to give such paleoecological information as past climates, water levels, water chemistry, abundance of aquatic macrophytes, and permanence of water bodies (Frey, 1964).

The stratigraphy of molluscs in Elk Lake will be discussed with respect to the faunal units recognized in the lake:

Unit A - Molluscs were found in this unit only in core 69-5. Only one complete mollusc shell was found, the snail Valvata tricarinata. Little paleoecological information can be derived from the occurrence of this snail since it is found living today in "many varying conditions in streams and lakes" and is widely distributed latitudinally, its range in North America extending from Great Slave Lake south to Virginia and the Ohio River (Baker, 1928).

Unit B - Fairly high numbers of snail shells and several Pisidium shells were found in both of the nearshore cores 69-2 and 69-3. The occurrence of mollusc shells in these cores at depths of over 8 m below the present water level represents a considerably

different depth distribution of molluscs than at present at the northern end of the lake, where few shells are found below 3.3 m depth. This may suggest a lower water level at that time, but the steeper slope of the bottom at that time (Plate 1) is a more probable explanation of the deeper occurrence of the shell zone, for at the steeply sloping southern end of the Elk Lake basin the shell zone is found today at a depth of 10 m. The species composition of mollusc shells in unit B and in all successive faunal units of these nearshore cores differs little from that of the present day, suggesting that the ecological conditions in the littoral zone of Elk Lake have not changed appreciably since that time. Inasmuch as the mollusc accumulations in the nearshore cores probably represent shell-zone deposits rather than life assemblages, they represent a random mixture of shells of molluscs that possibly lived in several different habitats within the littoral zone, as discussed above.

In the deeper-water cores 69-5 and C, the number of mollusc shells within unit B is quite high, compared to negligible quantities in all succeeding units. The fingernail clam, Pisidium, is almost the only mollusc represented in this unit in these cores. Because the species composition is very different from that of the nearshore cores, and because this clam is known to be able to live at considerable depths, it is assumed that it lived in situ and was not transported by water currents from the littoral zone. Such transportation would not be possible in the case of the 69-5 core, which came from the ridge. The occurrence of Pisidium at this depth in unit B suggests higher oxygen conditions in the lake at this time than in any following period. This conclusion corresponds to

the ecological interpretations made on the basis of chironomids, as discussed above.

Unit C - The nearshore cores 69-2 and 69-3 show a maximum in snail fossils in the middle of this unit. The correlation between finer sediment in the middle of the unit (silt rather than sand) and mollusc abundance seems to be related to an increase in aquatic plants, which form the substrate and food source of many snails, under these sediment conditions. Although no increase in plant seeds was found at this time, a distinct increase in plant-dwelling ostracods, Cypridopsis vidua and Cyclocypris sp., seems to support this assumption. The aquatic macrophytes may have been mainly Potamogeton species, which are poorly represented by fossil seeds in the sediments of Elk Lake at present. The increase in Pisidium in these cores in the upper part of unit C probably reflects the decrease in aquatic plants. In the deeper-water cores 69-5 and C, the decrease in Pisidium shells at the beginning of unit C suggests a decrease in the oxygen content of the lake. The single shell of the snail Valvata tricarinata in this unit in core 69-5 may represent transport of an air-filled shell by surface-water movements, as is probably true for all the snail shells found rarely at this depth in succeeding units.

Unit D - In the nearshore cores 69-2 and 69-3, numbers of mollusc shells decline considerably from the preceeding unit, perhaps because of the less steeply sloping bottom or because of a rise in water level. No molluscs were found in the deeper-water cores 69-5 and C in this unit.

Unit E - The increase in mollusc shells in most of the

nearshore cores at this time seems to represent an increase in productivity of the lake, confirmed by the stratigraphy of other plant and animal fossils. The increase in aquatic macrophytes, which may have been the main cause of increasing mollusc populations, is indicated by increases in seeds of aquatic plants. The stratigraphy of mollusc shells in the shallow-water cores corresponds to the sediment stratigraphy of shell-zone deposits discussed above, with possible interpretations of water movements which produced the stratigraphy. The few molluscs found in this unit in the deep-water cores probably represent transport in surface waters as discussed above.

AQUATIC MACROPHYTES

1. Ecology

Ecological studies of aquatic macrophytes have mainly been limited to shallow water, because of the problems involved in sampling in deep waters. Therefore ecological information concerning the factors controlling depth distributions of aquatic plants has been limited. The recent use of SCUBA in sampling deep-water aquatic vegetation has expanded the knowledge of depth distributions of aquatic plants and given a basis for speculation on the factors responsible for distributions. An intensive survey of the aquatic macrophyte flora of Long Lake in Itasca State Park was made recently by Schmid (1965) with the use of SCUBA and is a valuable contribution to the knowledge of the ecology of aquatic plants. He gives a review of earlier literature that is significant in aquatic macrophyte ecology.

Some of the major ecological factors controlling the distribution of aquatic macrophytes are:

1) Water chemistry

Water chemistry is an important factor in determining the floras of lakes. In Minnesota, the relationship between water chemistry and aquatic macrophyte floras has been studied by Moyle (1945). He concluded that water chemistry appears to be the most important single factor influencing the general distribution of aquatic macrophytes in Minnesota, even though the type of bottom soil and the physical nature of the body of water greatly influence the local distribution of species within its range of chemical tolerance. Moyle recognized three kinds of floras, which exhibited marked correlations with the chemical qualities of lake waters - soft-water

floras in northeastern Minnesota, hard-water floras in central and northern Minnesota, and alkali-water floras in southwestern Minnesota.

2) Temperature

The geographic distribution of aquatic plants is probably controlled largely by temperature. The knowledge of the present geographic distribution of aquatic plants represented in cores by macrofossil remains has led to significant interpretations of past climatic conditions in southeastern United States (Watts, 1970).

3) Substrate

Effects of substrate on the distribution of aquatic plants has been observed in several ecological studies of aquatic plants. Schmid (1965) noted that the texture of the substrate in Long Lake influenced the distribution of vegetation in extreme cases, i.e. a heavy layer of bark on the sediment, a cobble bottom, and a boulder bottom. Swindale and Curtis (1957) found correlations between the distribution of aquatic plants and the nature of the substrate when substrate "soils" were analyzed to determine their composition with respect to organic matter, marl, calcium, magnesium, nitrate, pH, and sand content.

4) Wave action

Schmid (1965) found only four species growing at the 0.5 m depth in his transects in Long Lake. Since all four species were narrow-leaved forms, he suggests that they may be adapted to withstand the strong wave action at this depth better than broad-leaved species. But frost was also suggested as a possible limiting factor at this depth since ice forms on the lake to a thickness of about

75 cm.

5) Light intensity and quality

Many of the observed changes in the abundance of aquatic plants with depth probably reflect changes in light intensity and quality, for aquatic plants probably vary in their light tolerance. Odum (1959) suggests that Chara is able to grow in deep water because of its tolerance to low light intensity. Some aquatic plants probably owe their deep-water distribution simply to their large size, which allows some of their photosynthetic structures to reach upwards into a zone having a light intensity high enough to enable plants to carry on photosynthesis.

6) Depth

It is difficult to ascertain the effect of depth alone as an ecological factor in plant distribution, for changes in depth are often accompanied by changes in other ecological factors, i.e. light intensity and quality, the nature of the substrate, and wave activity. Ruttner (1953) has pointed out significant studies of Gessner and Ferling, which have demonstrated the effect of hydrostatic pressure on submersed phanerogams. These plants, having a gas-filled intercellular system, are unable to thrive at an excess pressure of about one atmosphere, because various functions associated with their ventilation system are curtailed. Ruttner suggests that this explains why phanerogams, even in lakes of great transparency, do not reach a depth of 10 m, whereas plants without a gas-filled intercellular system, such as Chara, can extend considerably deeper.

Ecology of aquatic macrophytes in Elk Lake

The littoral zone of Elk Lake has a diverse flora and very

dense growth of aquatic macrophytes. Studies of the vegetation were made by the author in mid-July of 1968 and with the use of SCUBA by M. L. Whiteside in the summer of 1969. These studies, carried out mainly at the northern end of the lake near its outlet through Chambers Creek, showed the following distribution of plant species. The low-growing plants forming the dominant bottom cover of the lake were Najas flexilis and cf. Chara. Najas flexilis formed scattered clumps on sand close to the shore, extending out to a depth of about 50 cm, where it was replaced by cf. Chara as the dominant mat-forming plant. Beyond a depth of about 80 cm, the latter formed an almost continuous and very dense cover on the bottom of the lake, becoming less dense at about 2 m water depth and disappearing at about 3m. Accumulation of Lemna trisulca leaves washed to the shore by waves formed a thick mat in places. At one location, 2 m from the shore, this plant formed a mat 20 cm thick on the lake bottom. The alga Spirogyra also formed a thick deposit on the bottom in places.

Above the low mat-forming species rose the taller submerged and emergent plants. From the shore to a depth of about 1.5 m, there was considerable growth of these, including Potamogeton richardsonii, P. natans, P. zosteriformis, and several other species of Potamogeton, as well as Heteranthera dubia, Sparganium sp., Sagittaria sp., Ranunculus sp., Ceratophyllum demersum, Elodea canadensis, Myriophyllum sp., Zizania aquatica, Typha latifolia, Acorus calamus, and Scirpus validus/acutus. Beyond a depth of about 1.5 m, the tall vegetation became less dense, consisting mainly of scattered plants of Potamogeton praelongus, P. zosteriformis, and Ceratophyllum demersum, growing upward from the dense cf. Chara mat.

Beyond the cf. Chara mat, these species continued to grow to a depth of about 8 m, as observed by Whiteside while SCUBA-diving.

The ecological factors that seem to be most important in controlling the distribution of the aquatic plants in Elk Lake are:

1) Light

Most of the aquatic plant species of Elk Lake decline in abundance at about 1.5 m water depth, and cf. Chara falls off at about 3 m water depth. This depth distribution differs markedly from the distribution of a quite similar flora in nearby Long Lake, where aquatic macrophytes were still quite abundant at a depth of 5 m, and Nitella, which is closely related to Chara, extended to 11 m depth (Schmid, 1965). It may be suggested that the greater transparency of the water of Long Lake permits the deep growth of aquatic plants in that lake, while in Elk Lake low light intensity limits the depth distribution of aquatic macrophytes.

2) Water chemistry

The flora of Elk Lake falls into the "hard-water flora" category described by Moyle (1945). This flora is typical of lakes in central and northern Minnesota, where the calcareous gray glacial drift produces the typical water chemistry frequently associated with this flora - total alkalinity of 90-150 ppm, sulphate ion 5-40 ppm, and summer pH of surface waters 8.0-8.8. Moyle's description of the vegetation of hardwater lakes resembles the flora of Elk Lake very closely: "Hard-water lakes usually have a dense marginal zone of Chara spp., Potamogeton spp., Najas flexilis, Anacharis (Elodea) canadensis, Ceratophyllum demersum, and Myriophyllum exalbescens that often extends to a water depth of 8 to 10 feet." The typical

occurrence of Zizania aquatica, Scirpus validus, S. acutus, and Typha latifolia along shores and the growth of Lemna trisulca in quiet waters over fertile bottoms of hardwater lakes also apply to Elk Lake.

3) Substrate

Although light intensity may be a factor in causing the decline in aquatic plants at about 1.5 m, the presence of a marl bottom, which begins approximately at this depth, may also be suggested as a critical factor. Moyle (1945) observed that marl bottoms frequently have a flora limited to Chara spp., depauperate Najas flexilis, and Potamogeton pectinatus. The predominance of cf. Chara on the marl bench of Elk Lake may reflect this substrate limitation.

4) Wave activity

The sparseness of the flora of aquatic plants in very shallow water may be the result of the wave activity at the shore, as suggested by Schmid (1965) for Long Lake.

2. Distribution of fossils in surface sediments

The distribution of plant macrofossils in surface sediment has been considered by some paleoecologists in relation to the interpretation of plant-macrofossil stratigraphy (Watts and Winter, 1966; Argus and Davis, 1962). Although little actual research has been carried out, several generalizations have been suggested concerning the distribution of plant macrofossils in surface sediments of lakes and the degree to which the fossils represent the actual vegetation in and near the lake:

1) The distances that plant macrofossils are dispersed in lakes vary considerably, depending on the mode of dispersal and size of

the fossils. Since macrofossils are often relatively heavy, and water currents in lakes are usually ineffective in transporting heavy materials, the dispersal range of macrofossils is often limited (Watts and Winter, 1966).

2) The macrofossil counts may not be an accurate representation of vegetational communities in and near the lake, since some plants, especially annual plants, which produce large quantities of seeds, are over-represented, whereas low seed-producers are under-represented (Watts and Winter, 1966), and plants which reproduce by vegetative means are not represented at all.

3) Macrofossils may not represent local floras well if some or all taxa are not preserved. Preservation of macrofossils is known to be sensitive to conditions of sedimentation, and Argus and Davis (1962) suggest that the disappearance of a macrofossil in a core may reflect change in conditions of sedimentation rather than actual disappearance of the plant.

The study of the distribution of plant macrofossils in surface sediments of Elk Lake has made some contributions to the above generalizations of macrofossil distribution. The results of the transect studies are shown in Tables 5 and 6 and Figures 6-10. The following suggestions may be made through an analysis of these data:

1) Dispersal distances of macrofossils in Elk Lake

The distribution of plant macrofossils in Elk Lake suggest three categories with respect to modes and effectiveness of dispersal: a) Dispersal of heavy seeds and spores which are poorly adapted to floating. Figure 6 indicates the distribution of heavy seeds and spores in Elk Lake. Najas flexilis seeds and Chara sp. spores

[illegible]

Table 5. Numbers of seeds and spores in 100-cc samples of surface sediments from Elk Lake (transect shown in Figs. 7 and 9). Graphs of these data are shown in Figures 6 and 8.

| | Aquatic animal remains | | | | | Micro-sporophylls | | Bud scales | Bracts | Bark | Leaves of terrestrial plants | Leaves of aquatic plants | Needles |
|---|--|-----|----|-----|----|---|---|------------|--|---------------------------|------------------------------|---|--|
| | <u>Simocephalus ehippia</u> | | | | | <u>Abies/Picea/Pinus</u> <u>Larix laricina</u> | | Varied | <u>Betula papyrifera</u> <u>Populus tremuloides</u> | <u>Pinus cf. resinosa</u> | Other | <u>Betula sp.</u> <u>Myriophyllum sp.</u> <u>Chara sp.</u> Aquatic mosses <u>Lemna trisulca</u> | <u>Larix laricina</u> <u>Picea cf. mariana</u> <u>Pinus strobus</u> <u>Pinus banksiana</u> <u>Abies balsamea</u> |
| | <u>Daphnia ehippia</u> (partial) <u>Daphnia ehippia</u> (whole) Unidentified case 2 Unidentified case 1 | | | | | | | | | | | | |
| A | 7 | 7 | 2 | 38 | 4 | - | - | - | 1 | - | - | - | - |
| B | 1 | 3 | 1 | 2 | - | - | - | 1 | - | - | - | 56 | - |
| C | 4 | 38 | 11 | 54 | 3 | - | - | 1 | 1 | - | 3 | 17 | - |
| D | 2 | 56 | 24 | 22 | 11 | 2 | 1 | - | - | 3 | 1 | 5 | 3 |
| E | - | 110 | 58 | 8 | 14 | 1 | - | - | 1 | 1 | 1 | 6 | - |
| F | - | 98 | 38 | 18 | 10 | - | - | 4 | 3 | - | - | 6 | 4 |
| G | - | 153 | 83 | 5 | 21 | 2 | 2 | 1 | 5 | - | 5 | 2 | 3 |
| H | 1 | 152 | 87 | 6 | 16 | 1 | - | 4 | - | - | 1 | 3 | 1 |
| J | - | 10 | 52 | 1 | 6 | - | - | 1 | 2 | - | - | 2 | - |
| K | 3 | 45 | 58 | 6 | 23 | - | - | 4 | 2 | - | 1 | 4 | - |
| L | 2 | 61 | 47 | 6 | 14 | 5 | - | 1 | 4 | 1 | 1 | 6 | 1 |
| M | - | 153 | 53 | 64 | 25 | 1 | 3 | 4 | 1 | 1 | n | 9 | 3 |
| N | 5 | 200 | 52 | 114 | 91 | 3 | 1 | 9 | 2 | - | 1 | - | 2 |
| O | 1 | 173 | 82 | 85 | 26 | - | - | 7 | 5 | 1 | - | 7 | 4 |
| P | - | 35 | 35 | 5 | 13 | 1 | - | 3 | 4 | - | - | 1 | - |
| Q | - | 51 | 56 | 4 | 7 | - | - | 4 | - | - | 1 | 2 | - |
| 7 | - | 28 | 20 | 2 | 1 | - | - | 1 | 2 | - | - | 1 | - |
| 6 | - | 41 | 49 | 6 | 11 | 2 | - | 2 | - | 1 | - | 4 | - |
| 5 | - | 62 | 28 | 8 | 9 | 1 | - | 9 | 3 | 1 | - | 1 | - |
| 4 | 2 | 62 | 49 | 33 | 15 | 1 | 2 | 2 | 4 | 1 | 1 | 6 | 1 |
| 3 | 6 | 61 | 25 | 165 | 9 | 1 | - | 5 | 1 | 4 | - | n | 7 |
| 2 | 6 | 37 | 16 | 94 | 11 | - | - | 2 | - | 1 | - | n | 4 |
| 1 | 1 | 7 | 5 | 15 | - | 1 | - | 4 | - | - | - | n | 5 |

Table 6. Varied plant remains (100-cc samples) and animal remains (7-cc samples) in surface sediments from Elk Lake (transect shown in Figs. 7, 9, and 10) (n - numerous). Graphs of these data are shown in Figures 7, 9, and 10.

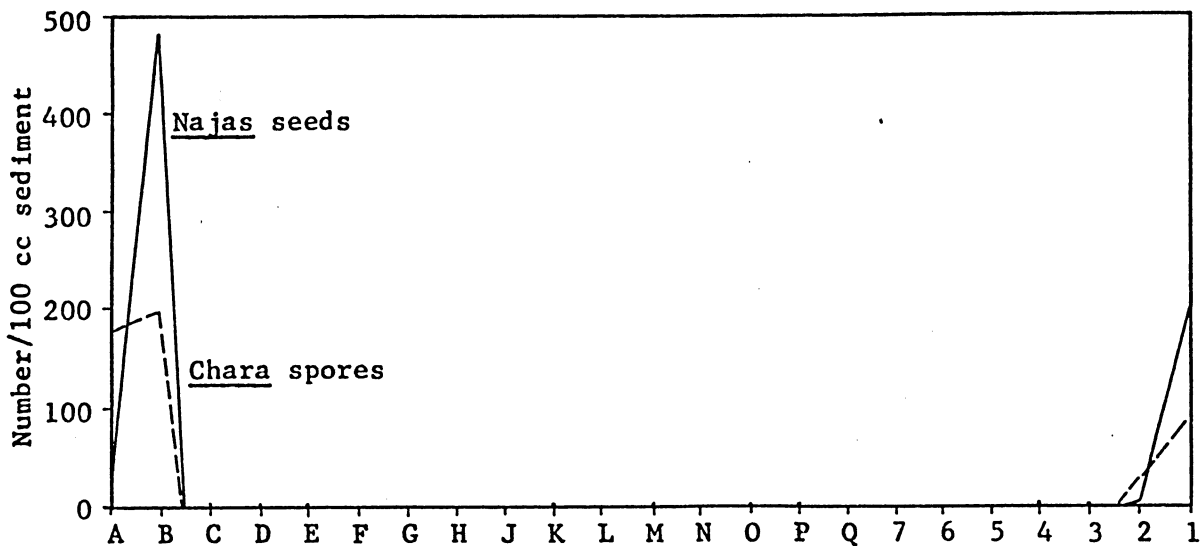


Fig. 6. Distribution of heavy seeds and spores in surface sediments of Elk Lake.

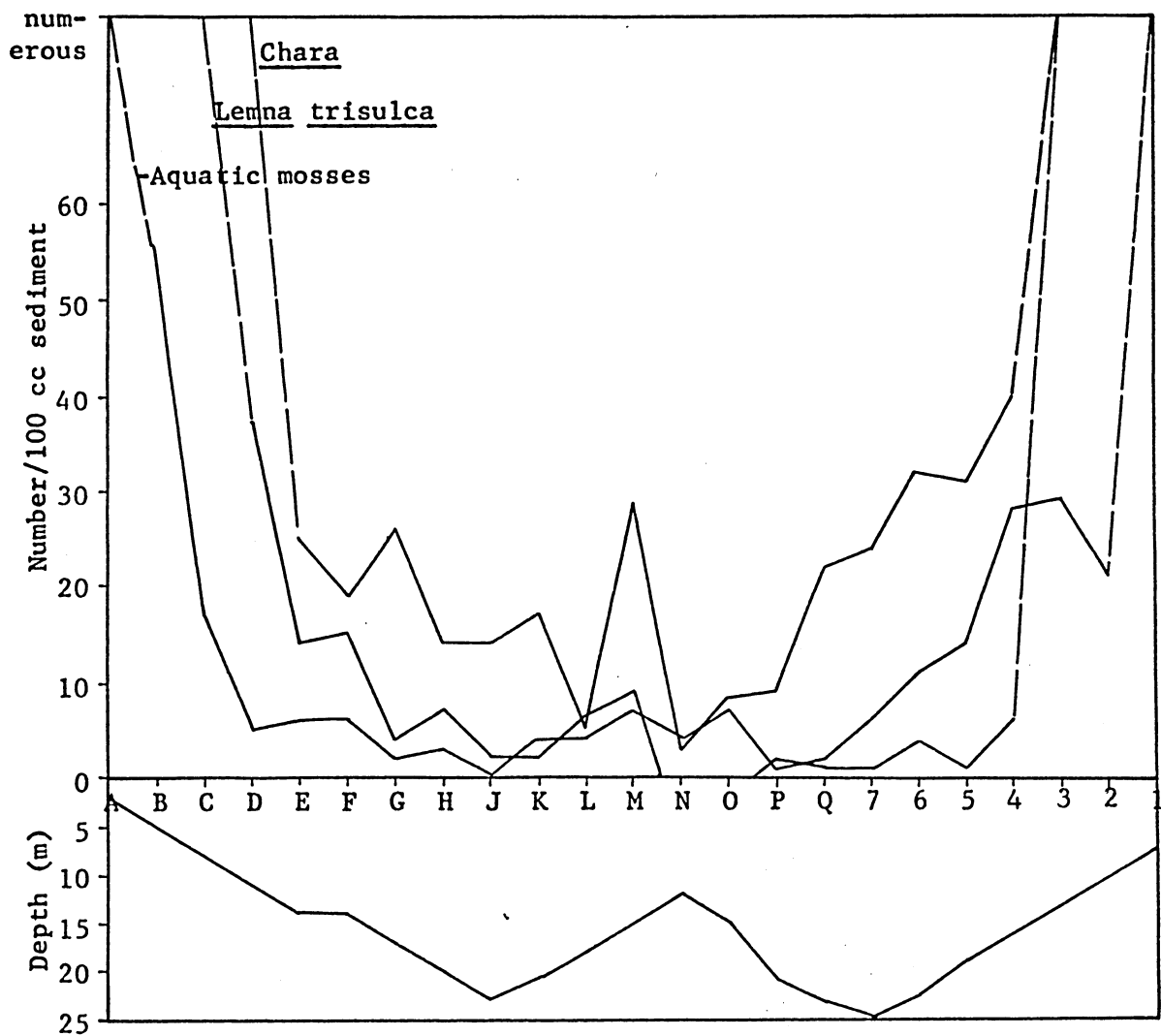


Fig. 7. Distribution of leaves of submerged aquatic plants in surface sediments of Elk Lake. Samples were taken along the transect shown in Fig. 2 (A at northern end) at the depths indicated.

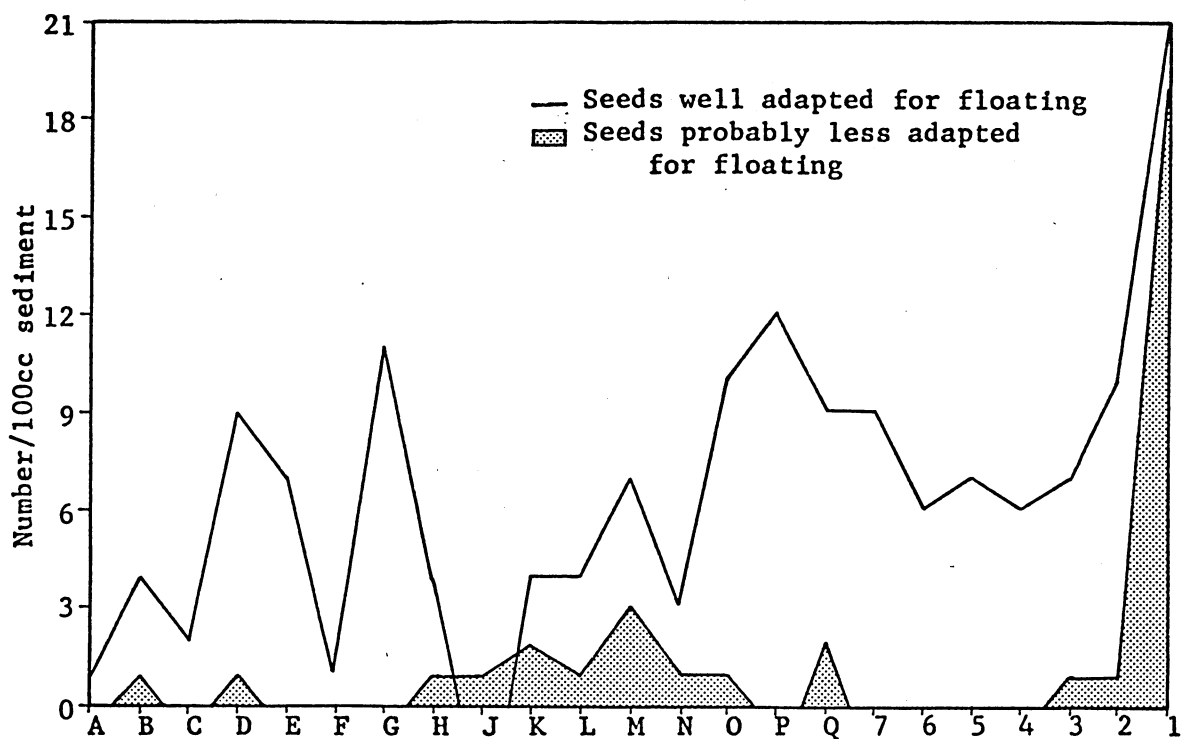


Fig. 8. Distribution of floating seeds in surface sediments of Elk L.

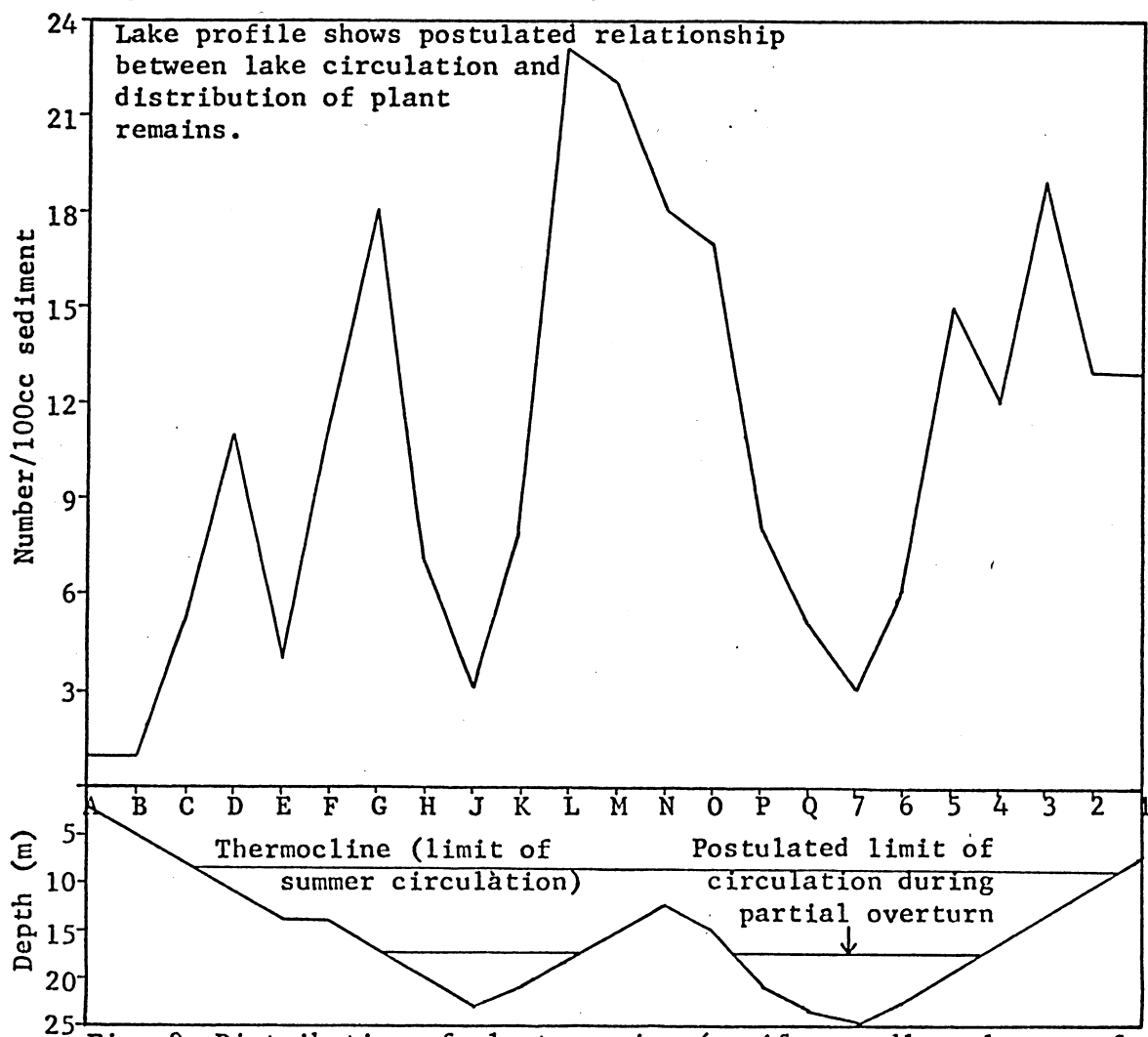


Fig. 9. Distribution of plant remains (conifer needles, leaves of terrestrial plants, bark, bracts, bud scales, and microsporophylls) in surface sediments of Elk Lake.

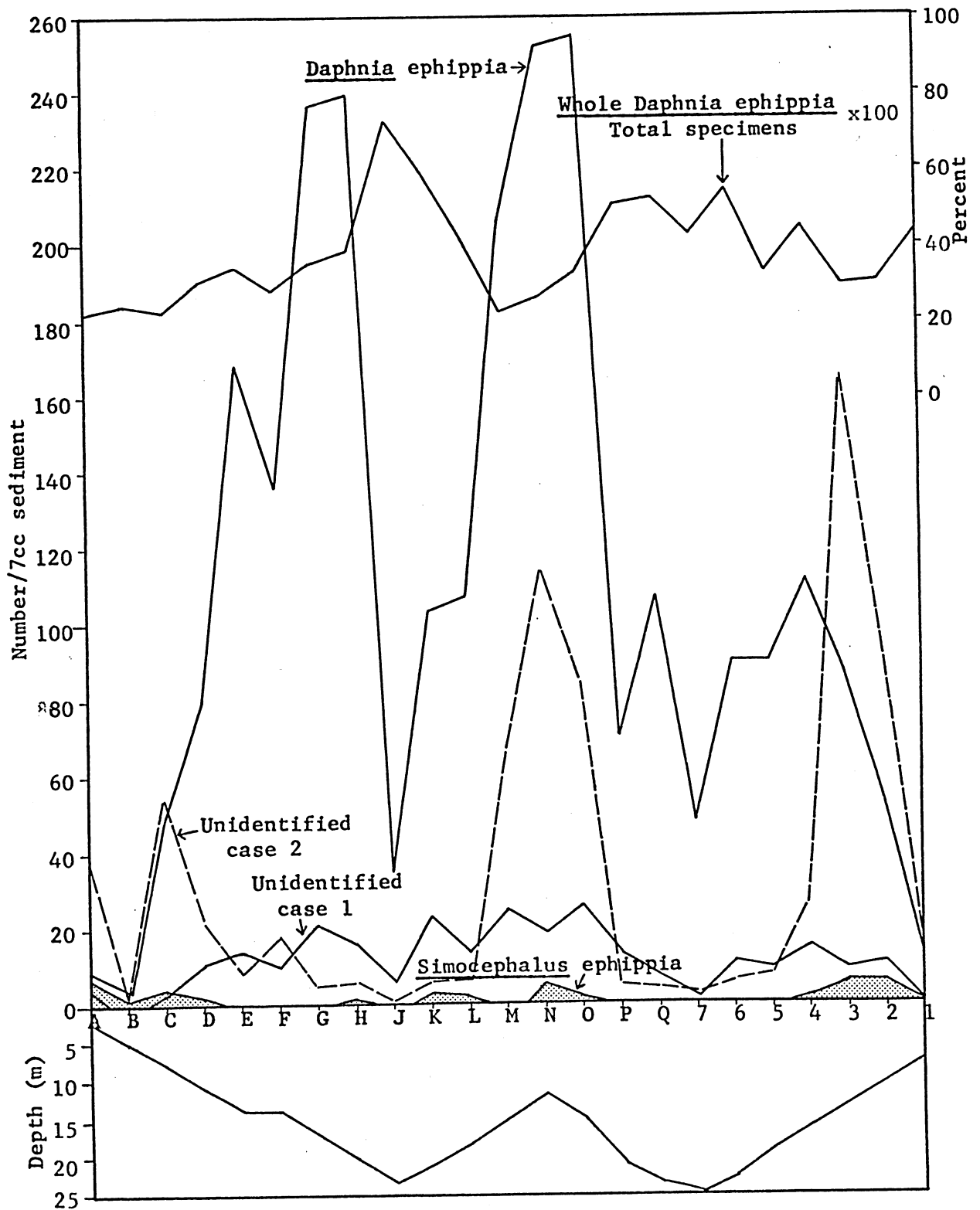


Fig. 10. Distribution of aquatic animal remains in surface sediments of Elk Lake.

are placed in this category, since they are highly concentrated near the shore and are very poorly represented in deep waters. Their distribution follows that of other shell zone fossils, suggesting that they are carried by wave-induced offshore currents to the depth of the shell zone and are deposited when bottom-water currents lose their carrying capacity.

b) Dispersal of macrofossils that exhibit some dispersal into deep water but are presumably poorly adapted for floating. Figure 8 indicates the distribution of seeds that seem to fall in this category, showing concentration of fossils near the south shore but small numbers of fossils in deep waters. Figure 7 shows a similar distribution for leaves of aquatic plants.

c) Dispersal of macrofossils that seem to be well-adapted for floating. Figures 8 and 9 indicate the distribution of seeds and other plant macrofossils that fall in this category, showing relatively high numbers of fossils across the lake basin, with less concentration of fossils at the shores. The seeds that are included in this distribution pattern have various adaptations for floating - extended pistils (Typha latifolia), possession of a pappus (Epilobium spp. and several Composites), wings (Betula papyrifera and several conifers), awns (grasses), and barbs (Bidens sp.). The dispersal of fossils adapted for floating is illustrated also by the distribution of the other plant remains indicated in Figure 9, including conifer needles, leaves of terrestrial plants, bark, bracts, bud scales, and microsporophylls of conifers. Macrofossils in this category, especially the plant remains included in Figure 9, seem to show concentrations in the shallow waters near the shore and on

the central ridge of Elk Lake, and low numbers of fossils in the two depressions. This distribution may result from the summer circulation pattern of Elk Lake after thermal stratification has been established (Fig. 9). The water currents in the epilimnion may be responsible for keeping light floating macrophytes within the epilimnion and preventing them from sinking into the hypolimnion. Thus, deposition of fossils would be concentrated on bottom sediments within the circulating epilimnion, as suggested by the macrofossil distribution observed in Elk Lake. But the concentrations of macrofossils extend to a depth of almost 20 m, while the epilimnion depth indicated by the oxygen stratification (Fig. 11) seems to extend only to 8-10 m. It may be suggested that water currents are also quite effective in the upper hypolimnion of Elk Lake, especially during the periods of overturn (Fig. 9).

The distribution of aquatic animal remains in Elk Lake (Fig. 10) seems to follow the same distribution pattern as that of floating plant macrofossils. Daphnia ephippia are the most abundant of these animal fossils and seem to illustrate this distribution pattern quite clearly. Daphnia live mainly in the epilimnion; their ephippia, containing eggs, are released at each molt and either sink to the bottom or float on the surface (Pennak, 1953). Floating egg sacs may be under the influence of currents in the epilimnion, as suggested for floating plant macrofossils, and their deposition may be concentrated in this zone. The condition of Daphnia ephippia, whether whole or partial, is recorded in Table 6, and the percentages of whole ephippia were calculated and graphed in Figure 10. There seems to be a higher percentage of whole ephippia in the deep

holes than in shallow water, possibly due to the greater weight of whole ehippia, which enables them to sink into the hypolimnion despite currents in the upper waters. However, the higher percentage of whole ehippia in deep waters may simply reflect unsuitable conditions for hatching of eggs, and thus whole ehippia are preserved. Although some cladocerans are able to withstand low oxygen concentrations, complete oxygen exhaustion during stratification limits cladoceran growth (Pennak, 1953). Wave action in shallow water could also account for broken ehippia. The other animal fossils indicated in Figure 10 include two unidentified objects that appear to be egg cases. Their distribution follows the same pattern as Daphnia ehippia, but it is not possible to determine whether they are floating eggs or belong to benthic animals.

The influence of epilimnion circulation on fossil distribution, suggested above as an explanation of the distribution of some plant and animal macrofossils in Elk Lake, has also been proposed by Davis (pers. com.) as an explanation for the distribution of fossil pollen in surface sediments of Frains Lake in Michigan. Oak pollen, being a relatively heavy grain, is presumed to sink into the hypolimnion and be deposited in deep waters, while lighter grains such as Ambrosia pollen are kept in suspension within the epilimnion and thus deposited mainly in shallow waters.

2) Preservation of macrofossils in Elk Lake

A comparison between the living community of aquatic macrophytes in Elk Lake and the occurrence of fossil seeds in surface sediments suggests that seeds of some species are not preserved. Potamogeton species, which predominate in the near-shore aquatic

macrophyte flora, were not represented by fossil seeds in any of the surface-sediment samples counted. The same situation was encountered in a similar study by the author in nearby Long Lake, where Potamogeton seeds were produced in considerable abundance and observed on surface sediments in late summer by a SCUBA diver. It may be suggested that Potamogeton seeds decay during the winter or are eaten by aquatic mammals or by water fowl. Many of the other species of aquatic plants that are quite abundant in the littoral aquatic macrophyte flora are also poorly represented by seeds in surface sediments.

3) Over-representation of aquatic plants in Elk Lake

The great abundance of fossil seeds of Najas flexilis in surface sediments is an excellent example of over-representation of a plant that is a relatively minor component of the aquatic macroflora. This species presumably produces high numbers of seeds which are well-preserved in surface sediments, undoubtedly due to their relatively firm wall structure.

3. Stratigraphy

In early stratigraphic studies of plant macrofossils, quantities usually were indicated by frequency symbols, but recent macrofossil studies have applied quantitative procedures (Watts and Winter, 1966). The counting and identification of plant macrofossils has been used to interpret past limnological conditions in several studies carried out in North America, including a study of Kirchner Marsh in Minnesota by Watts and Winter (1966) and an analysis of seeds from Pickerel Lake in South Dakota by Watts and Bright (1968). The present stratigraphic study of plant macrofossils in Elk Lake

cores is based on relatively small quantitative samples (5 cc of sediment usually) in comparison to 10-cm core segments used in the two studies cited above. Although relatively few seeds were found in the samples counted, some discussion of the seed stratigraphy in Elk Lake cores may be given. Several different kinds of seeds and spores were found in the seven Elk Lake cores analyzed for macrofossils, including low numbers of seeds of Typha, Betula, Pinus, Ranunculus, Juncus, Scirpus, Carex, Potamogeton, and Najas, and spores of two species of Chara. The most significant features of the stratigraphy of each faunal unit are:

Unit A - This unit is represented by plant macrofossils only in core 69-5, in which four Potamogeton seeds, one Ranunculus seed and one Betula seed were found in samples 1610 and 1620 cm near the base of the core.

Unit B - The most significant feature of the macrofossil stratigraphy in this unit is the occurrence of three Pinus seeds, which were not found in samples of any other unit. This faunal unit corresponds to the Picea and Pinus banksiana/resinosa-Pteridium pollen zones.

Unit C - Spores of a species of Chara are limited to this unit in shallow-water cores, but one specimen was found in unit A of the 69-5 core. Spores of the Chara species now living in the lake seem to be represented in all units except unit A.

Unit D - The high numbers of Najas flexilis seeds in this unit in core 69-3 is not well understood.

Unit E - The higher numbers of Chara spores and Najas flexilis seeds in this unit in cores 69-2 and 69-4 may reflect a general

increase in productivity in Elk Lake, as suggested by the study of other fossils.

Unit E' - The higher numbers of Najas flexilis seeds and Chara spores at a depth of 15-30 cm in the shallow-water short core (Plate 13) seems to reflect the lowering of the shell zone discussed above.

OSTRACODS

1. Taxonomy

Ostracods comprise a subclass of the class Crustacea of the phylum Arthropoda. They are distinguished by the dorsally hinged bivalved shell, which encloses the entire body, and the small number (4 or less) of pairs of postoral appendages (Hoff, 1942). Only one of the five orders (i.e. the Podocopida) of the Ostracoda has representatives in fresh water, the rest being strictly marine. The three superfamilies of this order are Cytheracea (chiefly marine), Cypridacea (both marine and freshwater), and Darwinulacea (entirely freshwater) (Moore et al, 1967). Members of all three of these superfamilies were found in the present study.

Taxonomic keys to ostracod species are based mainly upon structures of the body proper ("soft parts"). The key found in Ward and Whipple's Freshwater Biology (1918) makes use of the following characters: presence and length of natatory setae of the antennae, segmentation of the antennae, form and number of spines of the maxillary process, armature of the third thoracic leg, arrangements of the spermatid glands, and armature and shape of the furca. Since these parts were not present in most of the specimens found in the sediments, identification was based entirely upon features of the shell by comparison with published illustrations and descriptions.

The shape of the ostracod valves is one of the most important criteria used in identification; comparison with illustrations is extremely useful in this respect. But other criteria were considered in the present study in order to confirm identifications and to distinguish among species that are quite similar in shape. Size

of species is often useful is confirming identifications of Elk Lake ostracods, as in the case of the exceptionally large species Candona ohioensis. Color is not a useful distinguishing characteristic in the identification of the fossil valves, for most are colorless or almost so. Only Cyclocypris sp. is distinctively colored, being a deep yellow-brown. The distinctive coloration patterns found in many living ostracods is lost after death, for the color is contained in a thin membrane lining the inner surface of the relatively transparent valves. The membrane probably disintegrates soon after the death of the ostracod. The nature of the valve surface is distinctive in some species, i.e. Limnocythere and Cypria species. Muscle scars, marking the points of attachment of the transverse adductor muscles to the inner valve surfaces, are visible in most specimens, especially when viewed under a microscope at 100x magnification. These scars are not useful in identification beyond the genus level in most cases, for the pattern of scars is quite uniform within each genus.

Identification of ostracod species is commonly complicated by the presence of valves of immature molt stages. Ostracods grow by a succession of molts, during which the chitinous exoskeleton of both the body and the valves is removed (Furtos, 1933). There are usually nine instars in the ontogenetic development of most freshwater ostracods, only the last being sexually mature in most forms (Hoff, 1942). "At each molt, appendages increase in number and change in form and the shell also becomes altered in shape in various instars" (Hoff, 1942). In the present study, molt stages were observed in all species but were separated in the counts only in the Candona

species, for only in these were the molt stages readily separable by their size and morphology. Most of the other genera are smaller, and size differences between molt stages are therefore less distinct. In the largest Candona species, C. ohioensis, six instars were identified. If there are nine molt stages in the life history of this species, the other three molt stages were probably too small to be retained in the screens used for washing the sediment samples. Fewer molt stages were distinguished in the other Candonas. Superficial examination of the size differences among the molt stages of the various Candona species suggests that successive instars of each species increase in size according to a set ratio at each molt (i.e. by about 50%). In most Candona species, immature instars resembled the adult female more than the adult male, i.e. C. ohioensis and C. distincta. But in Limnocythere reticulata the later instars seemed to acquire the morphology of both the adult male and the adult female. In some species, however, immature instars bear little resemblance to either adult form. In such cases, the molt stages were assigned to certain species with considerable confidence on the basis of (1) size relationships to the adults of the species, (2) constant association with the adults in both surface sediments and cores, and (3) microscopic examination of the characteristic features of the valve surfaces.

The existence of morphological differences between male and female individuals of a species is a common feature in ostracods. This sexual dimorphism may initially present a problem to the observer in that it increases the number of different forms to be sorted out, but if both sexes of a particular species are identified in a

sample, greater confidence can be placed in the validity of the identification. The degree of morphological differentiation of the sexes varies in the ostracods, but there seems to be some constancy within the families:

Family Darwinulidae - Darwinula stevensoni, the only species of this family reported in North America, reproduces ordinarily by parthenogenesis, and males are usually absent (Hoff, 1942). In the present study, no males of this species were observed.

Family Limnocytheridae - Both male and female individuals of Limnocythere reticulata were identified in the present study. The male is longer but less high than the female and differs in shape. Females seem to be slightly more abundant than males. Sexes were not determined in L. sancti-patricii or in Cytherissa lacustris.

Family Candonidae - Most species within this group exhibit considerable morphological differentiation of sexes. Male and female individuals often differ in shape as well as size, males usually being larger than females. Females are generally more numerous than males in a population. These family characteristics were true for most of the species identified in the present study, i.e. C. ohioensis, C. acuta, C. distincta, C. decora, and C. truncata. But sexes were not distinguishable in C. albicans, C. punctata, and C. candida.

Family Cyclocypridae - In Cypria turneri and Physocypria pustulosa, sexes are similar but males slightly smaller (Hoff, 1942). No attempt was made to distinguish between the sexes of these species in the present study. No attempt was made to separate sexes of Cyclocypris sp. in the present study because sexes are usually similar (Hoff, 1942).

Family Cyprididae - Males of Cypridopsis vidua are unknown (Hoff, 1942) and were not observed in the present study. Males of Potamo-cypris smaragdina are usually found in small numbers (Hoff, 1942). Some were identified in the present study.

Identification of the ostracods found in the Elk Lake and Green Lake studies was based mainly upon the descriptions and illustrations given in Furtos (1933) and Hoff (1942). Most of the species found in the ostracod studies were described in these works, but some species, especially those confined to the lower portions of the Elk Lake cores, were not included. Several of these species were described by Staplin (1963a and b) in papers devoted to the "Pleistocene Ostracoda of Illinois". A few ostracod species could not be identified in any of these works. The following species were identified in the Elk Lake and Green Lake studies:

+ Candona acuta Hoff 1942

* C. albicans Brady 1864 (?)

* C. candida (O. F. Müller 1776) Vávra 1891

* C. caudata Kaufman 1900

- C. decora Furtos 1933

- C. distincta Furtos 1933

- C. elliptica Furtos 1933

* C. eriensis Furtos 1933

* C. leightoni Staplin 1963

- C. ohioensis Furtos 1933

- C. punctata Furtos 1933

* C. swaini Staplin 1963

- C. truncata Furtos 1933

References used in
identification:

- Furtos (1933)

+ Hoff (1942)

* Staplin (1963a)

= Staplin (1963b)

Swain (1963)

Candona sp.

= Cyclocypris sp.

+ Cypria turneri Hoff 1942

Cypria sp.

+ Cypricercus reticulatus (Zaddach 1844) Sars 1928

+ Cypridopsis vidua (O. F. Müller 1776) Brady 1867

* Cyprinotus glaucus Furtos 1933 (?)

= Cytherissa lacustris (G. O. Sars 1863) G. O. Sars 1925

+ Darwinula stevensoni (Brady and Robertson 1870) Brady and Norman 1889

= Ilyocypris gibba (Ramdohr 1808) Brady and Norman 1889 (?)

+ Limnocythere reticulata Sharpe 1897

L. sancti-patricii Brady and Robertson

+ Physocypris pustulosa Sharpe 1897

+ Potamocypris smaragdina (Vávra 1891) Daday 1900

2. Ecology

Since little intensive study has been devoted to the ecology of the ostracods of North America, their usefulness as paleoecological tools in Quaternary studies has been limited (Delorme, 1969). In the present stratigraphic study of Elk Lake, ostracod fossils are the most numerous of all the animal fossils studied and exhibit an interesting stratigraphy. It was therefore desirable to obtain as much information as possible concerning the ecology of the ostracod species found in the cores in order to interpret the past variations in ostracod communities in relation to past limnological changes within Elk Lake. The main sources of ecological information used in the present study were the publications of Hoff (1942), Furtos (1933), and Staplin (1963a and b). Some useful ecological

information concerning ostracods was also derived from several more general limnological studies dealing with several types of aquatic organisms.

The literature concerning ostracod ecology indicates that several questions seem to remain unanswered. Firstly, studies of ostracod ecology have yielded differing opinions concerning the existence of ostracod communities as such. A community may be defined as an aggregate of organisms that forms a distinct ecological unit, having a more or less uniform species composition and occurring in a particular habitat (Kendeigh, 1961). Communities may be defined in terms of all organisms present (biotic community) or of selected types of organisms, i.e. ostracod community. It is quite well established that different ostracod communities exist in distinctly different aquatic habitats. Furtos (1933) reports that "in Lake Erie there is a fauna characteristic of the mud-bottom at a depth of twenty-five feet or more, another is characteristic of the quiet, shallow, weedy inlets; and still another characteristic of stony bars and rock pools". Moore (1939) and Cole (1955), in their general limnological studies of microbenthos of lakes, list ostracod species as littoral, sublittoral or profundal, or combinations of these. Hoff (1942) found different ostracod communities living in Illinois in temporary still waters, permanent still waters, temporary running waters, and permanent running waters.

Although the above information indicates that community differences on a large scale are easily recognizable, there has been considerable discussion concerning the existence of ostracod communities on a smaller scale, especially within the vegetated zones of

ponds, streams, and lakes. Some authors classify ostracod species according to their habitat preferences — free-swimming, creeping on water plants or ooze, and burrowing in the slime or ooze (Ward and Whipple, 1918). But Hoff (1942), in his collections from shallow ponds and streams and from the littoral zone of the larger bodies of water, states that he found little difference in the species composition of samples collected from bare bottom, grass, aquatic vegetation, alga, decaying vegetation and plankton, although a few species seem to show higher incidence on bare bottom or as a constituent of plankton than others.

Another question that requires study is the elucidation of the factors responsible for limiting the habitat distribution of ostracod species, and therefore of communities. Internal factors, especially locomotive capacities, have been suggested as an important factor in allowing some species to be free-swimming while others are confined to the sediments or plants. There has been considerable discussion concerning the factors responsible for the depth distribution of ostracods. Many possible limiting factors have been suggested, including differences in substrate, temperature, light, water chemistry, oxygen content, hydrogen-ion content, water pressure, and food.

The present studies of ostracod ecology in Elk Lake and Green Lake were designed to contribute to an understanding of these problems. The ecology of ostracods was studied by the four methods discussed earlier — collection of living ostracods in surface sediments, collection of living ostracods in open water, collection of living ostracods associated with aquatic plants, and ecological

| Subcommunities | | | OSTRACODS | | | | | | | | | | | | | MOLLUSCS | | | | | | | |
|----------------|-------------------------------|-----------|-----------------------|-------------------|------------------------------|--------------------------|------------------------|-----------------------------|--------------------------|----------------------|-------------------------|-----------------------|--------------------------|------------------------|--------------------------|------------------------|---------------------------|------------------|----------------------|------------------------|----------------------|----------------------|----------------------------|
| Sediment type | | Depth (m) | <u>Cypria turneri</u> | <u>Cypria sp.</u> | <u>Physocypria pustulosa</u> | <u>Cypridopsis vidua</u> | <u>Cyclocypris sp.</u> | <u>Darwinula stevensoni</u> | <u>Candona ohioensis</u> | <u>Candona acuta</u> | <u>Candona truncata</u> | <u>Candona decora</u> | <u>Candona elliptica</u> | <u>Candona candida</u> | <u>Candona distincta</u> | <u>Amnicola limosa</u> | <u>Marstonia lustrica</u> | <u>Physa sp.</u> | <u>Pisidium spp.</u> | <u>Gyraulus parvus</u> | <u>Sphaerium sp.</u> | <u>Ferrisia spp.</u> | <u>Valvata tricarinata</u> |
| a | Sand | 0.5 | - | - | 25 | 6 | - | 11 | 1 | - | - | - | - | - | - | 3 | 7 | - | 3 | - | - | - | - |
| | | 0.7 | - | - | 47 | 5 | 3 | 3 | 2 | 2 | - | - | - | - | - | - | 6 | 3 | - | 9 | - | - | - |
| | | 1.0 | - | - | 8 | 1 | - | 2 | 5 | 2 | - | - | - | - | - | - | 1 | 1 | - | - | - | - | - |
| b | Black gyttja | 1.0 | 7 | 11 | 13 | 1 | - | - | 6 | 2 | 4 | - | - | - | - | 5 | 1 | 1 | - | - | - | 1 | - |
| | | 1.4 | - | 1 | 4 | 1 | - | - | 1 | - | 2 | - | 1 | - | - | - | - | - | - | - | - | - | - |
| | Shell zone | 2.0 | 2 | 2 | 4 | - | - | - | 3 | 7 | - | - | 1 | 1 | - | 1 | 1 | - | 2 | 1 | - | - | - |
| | | 3.3 | 3 | - | 15 | - | - | 2 | 8 | 7 | - | 2 | - | 11 | - | 1 | - | - | 3 | - | - | - | 4 |
| | | 3.7 | - | 3 | - | 5 | 2 | - | 2 | 9 | 14 | - | - | 3 | 1 | 5 | 2 | 5 | - | 11 | - | - | - |
| c | Black gyttja with plant frag. | 4.2 | - | - | 2 | - | - | - | - | - | - | - | 2 | 1 | - | 2 | - | 1 | - | - | - | - | - |
| | | 5.0 | 6 | - | 6 | 2 | 2 | 48 | 6 | 2 | - | - | - | 2 | - | - | - | - | 2 | - | - | - | - |
| | | 5.3 | - | - | - | - | - | 4 | 5 | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - |
| | | 5.9 | 1 | - | 2 | - | - | 7 | 8 | - | - | - | 2 | - | - | - | - | - | - | - | - | - | - |
| d | Black gyttja | 6.0 | 2 | - | 2 | - | - | 3 | - | - | - | - | - | - | - | - | - | - | 3 | - | - | - | - |
| | | 6.9 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | | 7.3 | 3 | - | 3 | - | - | - | 5 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | | 7.7 | 8 | 1 | - | - | - | - | 9 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | | 8.3 | - | - | 2 | - | - | - | 2 | - | - | - | - | - | - | - | 2 | - | - | - | - | - | - |
| | | 8.6 | 1 | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | | 9.3 | 2 | - | 3 | - | 3 | - | 5 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | | 10.3 | 2 | - | - | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - |
| | | 12.0 | 3 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | | 12.5 | - | - | 1 | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - |
| | | 16.7 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | | 19.5 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| e | | 12.3 | - | - | - | - | - | 5 | - | - | 7 | - | - | - | - | - | - | - | - | - | - | - | |
| Rock at shore | | | 1 | - | 25 | 32 | 4 | - | - | - | 7 | - | 2 | - | - | 3 | 2 | - | - | 2 | - | - | - |

Subcommunities of benthic community: a - Near-shore sand subcommunity
b - Dense-vegetation subcommunity
c - Sparse-vegetation subcommunity
d - Sublittoral-profundal subcommunity
e - Ridge subcommunity

Table 7. Numbers of living ostracods and molluscs in samples of surface sediments from Elk Lake taken from the northern end of the lake (on transect of Fig. 2) on June 13 and June 25, 1969. Numbers indicate animals/30cc sediment except in samples 6.9, 8.6, 10.3 (60cc); 12.5 (45cc); 16.7 (50cc); and 19.5 (75cc). Graphs of these data are shown in Plates 4 and 5.

| Date | Water depth (ft) | Plant species | OSTRACODS | | | | | | | MOLLUSCS | | | |
|---------------|------------------|--|--------------------------|------------------------|------------------------------|--------------------------|----------------------|-------------------------|--------------------------|------------------------|------------------------|----------------------------|------------------|
| | | | <u>Cypridopsis vidua</u> | <u>Cyclocypris</u> sp. | <u>Physocypria pustulosa</u> | <u>Candona ohioensis</u> | <u>Candona acuta</u> | <u>Candona truncata</u> | <u>Candona elliptica</u> | <u>Amnicola limosa</u> | <u>Gyraulus parvus</u> | <u>Valvata tricarinata</u> | <u>Physa</u> sp. |
| June 25, 1969 | 25 | <u>Ceratophyllum demersum</u> | 7 | - | - | - | - | - | - | 9 | 1 | - | 14 |
| | 13-15 | <u>C. demersum</u> | 53 | 7 | - | - | - | - | - | 34 | 4 | 2 | 11 |
| | 15 | <u>Potamogeton praelongus</u> | 46 | 31 | - | - | - | - | - | 32 | 2 | - | 2 |
| | 13-15 | <u>P. zosteriformis</u> | 3 | 1 | - | - | - | - | - | 4 | - | 1 | - |
| | 15-20 | <u>P. zosteriformis</u> | 12 | 6 | - | - | - | - | - | 14 | 1 | 3 | 2 |
| | * 12 | Debris below <u>Elodea</u> | 19 | 9 | 4 | 1 | 2 | - | 1 | - | - | - | - |
| June 28, 1969 | 5-7 | <u>Elodea canadensis</u> | 4 | - | - | - | - | - | - | 2 | - | - | 1 |
| | 5-7 | <u>Chara</u> sp. | 8 | - | - | - | - | - | - | - | 2 | - | 8 |
| | 5-7 | <u>Potamogeton praelongus</u> | 65 | - | 1 | - | - | - | - | 18 | - | - | 10 |
| | 5-7 | <u>P. zosteriformis</u> | 13 | - | - | - | - | - | - | 4 | 1 | - | - |
| | * 1 | <u>P. illinoensis</u> | - | - | 1 | - | - | - | - | - | 1 | - | 1 |
| | * 6 | <u>Scirpus validus/acutus</u> | 4 | - | - | - | - | 2 | - | - | - | - | - |
| | * 1 | <u>Zizania aquatica</u> | 3 | 1 | 3 | - | - | 1 | - | - | 22 | 1 | 9 |
| | * 6 | <u>Chara</u> sp., <u>Lemna tri-sulca</u> and algae mat | 94 | 35 | 1 | - | - | 34 | - | - | 9 | - | 3 |

Table 8. Numbers of living ostracods and molluscs in bagged plant samples collected by SCUBA at the northern end of Elk Lake on June 25, and June 28, 1969. Starred samples have been assigned to the low vegetation subcommunity of the plant-associated ostracod community, while the rest of the samples belong to the tall-plant subcommunity. Data for Cypridopsis vidua and Cyclocypris sp. are shown in Plate 4.

| Subcommunities of benthic community | | Depth (ft) | OSTRACODS | | | | | | | | MOLLUSCS | | | | |
|--|-----|------------|-----------------------|-------------------|------------------------------|--------------------------|--------------------------|----------------------|--------------------------|------------------------|-------------------------|------------------------|---------------------------|------------------|---------------------|
| | | | <u>Cypria turneri</u> | <u>Cypria sp.</u> | <u>Physocypria pustulosa</u> | <u>Cypridopsis vidua</u> | <u>Candona ohioensis</u> | <u>Candona acuta</u> | <u>Candona elliptica</u> | <u>Candona candida</u> | <u>Candona albicans</u> | <u>Amnicola limosa</u> | <u>Marstonia lustrica</u> | <u>Physa sp.</u> | <u>Pisidium sp.</u> |
| a - Littoral | 5 | - | - | - | - | - | - | - | 2 | - | - | 1 | 1 | 1 | 1 |
| | 8 | - | - | 11 | 3 | - | 4 | 1 | 8 | 2 | - | - | - | - | - |
| | 11 | 2 | 1 | - | 2 | - | 6 | - | 1 | - | 1 | - | - | - | - |
| | 13 | 2 | 1 | 2 | - | 2 | 1 | - | 2 | - | 4 | 1 | - | - | - |
| | 20 | 2 | - | - | - | - | 2 | - | - | - | - | - | - | - | - |
| | 25 | 2 | - | 8 | - | 11 | 1 | 2 | 1 | - | - | - | - | - | - |
| b - Sublittoral- (profundal) | 30 | 17 | - | 3 | - | 9 | - | - | - | - | - | - | - | 2 | - |
| | 40 | 4 | 1 | 7 | - | 3 | 3 | - | - | - | - | - | - | - | - |
| | 50 | 5 | - | 11 | - | 1 | - | - | - | - | - | - | - | - | - |
| | 67 | 5 | - | 7 | - | 1 | 2 | - | - | - | - | - | 1 | 12 | - |
| | 77 | 5 | 4 | 3 | - | - | - | - | - | - | - | - | - | 1 | - |
| | *96 | 2 | 2 | - | - | - | - | - | - | - | - | - | - | - | - |
| Ridge | 3 | - | - | 4 | - | 2 | 1 | 1 | 2 | - | 1 | - | - | 2 | - |

Table 9. Numbers of living ostracods and molluscs in samples of surface sediments from Green Lake collected on June 24, 1969. Samples consisted of 15 or 20 cc of sediment, but all numbers on the table indicate animals/15 cc sediment (except starred sample which is a water sample taken just above the sediment surface).

| | | | | | |
|---|---------|--|---------------------|--------|--|
| Temperature Profile (Water depth of 30 m at sampling location) | | | Weather Conditions: | | |
| Surface | 17.0°C | | Air temperature | 21.0°C | |
| 1-2 m | 16.6 | | Scattered clouds | | |
| 3 m | 16.5 | | Strong wind | | |
| 4 m | 16.4 | | | | |
| 5-14 m | 16.3 | | | | |
| 15-20 m | 16.2 | | | | |
| 21-30 m | 16.1 | | | | |
| Oxygen Profile (Water depth of 26 m at sampling location) | | | | | |
| Surface | 8.8 ppm | | | | |
| 25 m | 8.4 ppm | | | | |

Table 10. Temperature and oxygen data for Green Lake on June 24, 1969.

inferences made on the basis of distribution of fossil remains of ostracods in surface sediments. The data obtained in these studies are shown in Tables 7-11, Fig. 11, and Plate 4. Examination of these data results in the following suggestions concerning ostracod communities and their controlling factors in Elk Lake and Green Lake.

Classification of ostracod communities in Elk Lake and Green Lake:

The following classification is proposed on the basis of data collected in the present study. Since the samples were collected in June of 1969, some variations in species composition and relative abundance may be expected during different seasons and possibly from year to year. Species lists may not be complete, especially for Green Lake, from which only a small number of samples was examined. In Elk Lake, studies of fossil ostracods in surface sediments helped to complete species lists, but they are not included in the following classification. In Green Lake, only the sediment community was studied, so the classification for that lake includes data only in that community. Predominant species are listed in order of abundance, and "other" species in order of taxonomic classification in Hoff (1942).

Ostracod Communities of Elk Lake

1. Plant-associated Ostracod Community

a) Tall-plant subcommunity

Dominant species - Cypridopsis vidua, Cyclocypris sp.

Other species - Physocypria pustulosa

b) Low-plant subcommunity

Dominant species - Cypridopsis vidua, Cyclocypris sp.

Other species - Candona acuta, C. elliptica, C. ohioensis,
C. truncata, Physocypria pustulosa

2. Benthic Ostracod Community

a) Near-shore sand subcommunity (0-1 m water depth)

Dominant species - Physocypria pustulosa, Darwinula stevensoni

Other species - Candona acuta, C. candida, C. ohioensis,
Cyclocypris sp., Cypridopsis vidua

b) Dense-vegetation subcommunity (1-4 m water depth)

Dominant species - Physocypria pustulosa, Candona acuta,
C. ohioensis

Other species - Candona candida, C. decora, C. distincta,
C. elliptica, C. truncata, Cyclocypris sp., Cypria turneri,
Cypria sp., Cypridopsis vidua, Darwinula stevensoni

c) Sparse-vegetation subcommunity (4-6 m water depth)

Dominant species - Darwinula stevensoni, Candona ohioensis

Other species - Candona acuta, C. candida, C. elliptica,
Cyclocypris sp., Cypria turneri, Physocypria pustulosa,
Cypridopsis vidua

d) Sublittoral-profundal subcommunity (6-12.5 m water depth)

Dominant species - Candona ohioensis, Cypria turneri

Other species - Candona acuta, C. decora, Cyclocypris sp.,
Cypria sp., Physocypria pustulosa

e) Ridge subcommunity

Dominant species - Candona decora, C. ohioensis

Ostracod Communities of Green Lake

Benthic Ostracod Community

a) Littoral subcommunity (0-8 m water depth)

Dominant species - Physocypria pustulosa, Candona candida,
C. acuta

Other species - Candona elliptica, C. albicans, Cypria turneri,
Cypria sp., Cypridopsis vidua, Candona ohioensis

b) Sublittoral-(profundal) subcommunity (maximum water depth 8 m)

Dominant species - Cypria turneri, Physocypria pustulosa

Other species - Candona acuta, Cypria sp., Candona ohioensis

The criterion used in the differentiation of communities was the "50% rule", which states that "two aggregations of species occurring naturally in different areas or in the same area at different times are to be considered as distinct communities when at least 50% of the predominant species of each aggregation are, if not exclusive, at least characteristic to the aggregation" (Ken-deigh, 1961). "Predominant species" are the most numerous constituents of a community and are distinguished from the less important "member species" by an arbitrary dividing line. A species is considered to be "exclusive" when it occurs only in a single area, habitat, or community and "characteristic" when it is abundant in one area or community but also occurs in small numbers elsewhere. Ken-deigh suggests that the 50% rule is preferable to the more involved statistical criteria for differentiating communities in the light of present ecological knowledge. In the Elk Lake study, the application of the 50% rule resulted in the recognition of only two ostracod communities — a plant-associated community and a benthic community. But considerable differences in species composition were noted within each community, making subdivision into subcommunities desirable. Subcommunities exhibited some differences in predominant

species (but less than 50% difference) as well as some distinct variations in the "member species". (In the classification, member species are included in the term "other species", for some of the ostracods found in samples may not be regular members of the community). In Green Lake, only the benthic ostracod community of those that may possibly occur was studied. Fewer subcommunities were recognized in the Green Lake benthic community than in the same community in Elk Lake.

Ostracod communities and subcommunities distinguished by their species composition were found to correspond quite well with divisions of the habitat in Elk Lake and Green Lake. This helped to confirm the validity of the communities and subcommunities described and provided a simple system of naming the communities and subcommunities on the basis of habitat, as suggested by Kendeigh (1961).

It is interesting to note that the two ostracod communities recognized in Elk Lake, differentiated on the basis of their species composition by the 50% rule, also exhibit different life-forms. Life-form refers to the general shape or appearance of an organism and is often used as the primary basis of community recognition on a large scale, i.e. forest versus grassland. In Elk Lake, the predominant species of the plant-associated ostracod community, Cypripopsis vidua and Cyclocypris sp., are both active swimmers with small, plump shells. Most of the benthic ostracods are more compressed laterally, permitting them to burrow more efficiently in the sediments, and are poor swimmers.

Description of Ostracod Communities and Subcommunities in Elk Lake
and Green Lake:

Elk Lake

1. Plant-associated Ostracod Community

All ostracod samples collected by plant bagging (Table 8) were included in this ostracod community, because all exhibited a predominance of Cypridopsis vidua and Cyclocypris sp., a species composition very much different from that of all sediment samples. The 50% rule confirms the differentiation of these two communities, since more than 50% of the predominant species of each aggregation are characteristic of the aggregation. Within the plant-associated ostracod community, two subcommunities were recognized on the basis of the presence and abundance of other species in the samples, and confirmed by a habitat difference between the two subcommunities. The "tall-plant subcommunity" consists almost entirely of the two predominant species, while in the "low-plant subcommunity" other species, typical of the benthic community, were also present. Thus, the latter subcommunity seems to represent a transition between the plant-associated community and the benthic community.

The clear distinction between plant-associated and benthic ostracod communities in Elk Lake represents a view entirely different from that of Hoff (1942), who concluded from his ecological studies in Illinois that ostracods show little preference for either vegetation or bare bottom. Hoff's conclusion seems to differ as a result of the following factors: 1) Hoff's conclusions were based on frequency data rather than on actual counts, as in the present study. This method does not give an accurate view of ostracod selectivity

to certain habitats, since abundance is not considered. In the present study of Elk Lake, vegetation samples collected in shallow water or near the sediment surface usually contain only low numbers of benthic species, while typical plant-associated species are dominant. Most sediment samples contain small percentages of plant-associated species, probably as contaminants from the dense vegetation above the sediment. If frequency alone were considered, the "low-plant" samples and the sediment samples would be very similar, whereas abundance data indicate considerable differences. Since most of Hoff's samples were collected in shallow water, it is not surprising that frequency data did not bring out habitat selectivity. 2) Although most of Hoff's vegetation samples were probably taken in shallow water and were probably contaminated with benthic species, the sixteen samples of aquatic vegetation collected by Bertrand A. Wright (in Hoff, 1942) contained mainly three species: Cypridopsis vidua, Potamocypris smaragdina, and Limnocythere verrucosa, with Cyclocypris forbesi and Physocypris pustulosa each recorded in only one sample. Perhaps these samples were taken in higher vegetation and thus were not contaminated so much with typical benthic species.

Although at least two species of ostracods seem to show definite preference for an aquatic-plant habitat in Elk Lake, there seems to be no selectivity for particular species of aquatic plants. The ratio between Cypridopsis vidua and Cyclocypris sp. abundance exhibits considerable variation in the samples, but there seems to be no definite correlation with the particular species of aquatic plants with which they are associated. Hoff (1942) reached the same

conclusion in a similar study.

a) Tall-plant subcommunity

i) Species composition

All samples of aquatic vegetation collected more than about 30 cm above the sediment surface exhibit a strong dominance of Cypridopsis vidua and Cyclocypris sp. Only one other species, Physocypris pustulosa, was represented in the samples, and this by only one individual.

ii) Habitat factors controlling species composition

The abundance of Cypridopsis vidua and Cyclocypris sp. in the upper waters of the littoral zone is doubtless related to their well-developed swimming setae, which make these species more active swimmers than most ostracod species. Hoff (1942) records that in the genus Cypridopsis "swimming setae of the antennae are well-developed and in the genus Cyclocypris "swimming setae of both antennules and antennae are long and well-adapted for swimming". The active swimming ability of Cypridopsis vidua and Cyclocypris sp. was confirmed by the data obtained in the live trap studies (Table 11). In the traps, designed so that only active swimmers could enter, these species were found to be predominant in the counts.

| | E10 | E9 | E8 | E7 | E6 | E5 | E4 | E3 | E2 | E1 |
|------------------------------|-----|----|----|----|----|----|----|----|----|----|
| <u>Cypria turneri</u> | - | - | - | - | - | - | - | - | - | 1 |
| <u>Cypria</u> sp. | - | - | 1 | - | - | - | - | 1 | - | - |
| <u>Physocypris pustulosa</u> | 5 | 6 | 1 | - | 5 | - | 1 | - | 1 | - |
| <u>Cypridopsis vidua</u> | 29 | 7 | 10 | 1 | 16 | 5 | 3 | 4 | 5 | 3 |
| <u>Cyclocypris</u> sp. | 14 | 24 | 2 | 1 | 16 | 1 | - | - | - | - |
| <u>Amnicola limosa</u> | - | 1 | - | - | - | - | - | - | - | - |

Table 11. Numbers of ostracods and molluscs in live traps set up 1 m above the sediment in the littoral zone at the northern end of Elk Lake by M. C. Whiteside in late summer of 1969. E1-E10 represent samples taken along a transect from water depths of 22 ft to 9 ft.

The dominant species of the tall-plant subcommunity of Elk Lake, Cypridopsis vidua and Cyclocypris sp., probably also occur occasionally in the plankton of the lake as "adventitious planktonts", apparently being carried out by water currents from their normal habitats in the littoral zone (Hoff, 1942). Cypridopsis vidua was reported in plankton samples taken by Hoff (1942), but Cyclocypris was not found, probably because it is rare in Illinois. In Elk Lake, the considerable numbers of fossil valves of both Cypridopsis vidua and Cyclocypris sp. in deep-water sediments across the entire lake basin (Plate 4) suggests that these species were carried as "adventitious planktonts", for almost no living individuals were found in the sediment samples beyond a depth of 5 m. The occurrence of these two species as adventitious planktonts may be related to their swimming ability as suggested above, or it may be simply the result of their location in the upper waters of the littoral zone, where they are more subject to being transported into deep water by water movements than ostracod species confined to the sediment or a narrow zone above the sediment surface.

b) Low-plant subcommunity

i) Species composition

The predominant species, as in the tall-plant subcommunity, are Cypridopsis vidua and Cyclocypris sp., but several other species were found in the samples as well. Physocypria pustulosa and Candona truncata were each found in over half of the samples, in considerable abundance in some of the samples.

ii) Habitat factors controlling species composition

The samples assigned to this subcommunity were collected near

the sediment surface (within about 30 cm) (Table 8) in several types of aquatic macrophyte, viz. in a mat of Chara, Lemna, and algae and in decaying vegetation. The dominance of Cypridopsis vidua and Cyclocypris sp. in these low-plant samples is not unexpected, because these two species are always associated with aquatic plants. The occurrence of the other species in the samples, however, requires discussion. The presence of Physocypria pustulosa in several of the samples, especially in the Zizania aquatica sample, is easily explained because this species is a good swimmer (Hoff, 1942). Hoff found this species as one of the two ostracod species reaching the highest incidence in his plankton samples. The occurrence of Candona spp. in the low-plant samples is more difficult to explain, because most Candonas are typically benthic in habitat. The lack of swimming setae on the antennae of members of this genus indicates that they are creeping and burrowing forms (Hoff, 1942). The low percentages (3-6%) of Candona ohioensis, C. acuta, and C. elliptica in one of the samples may be the result of contamination of the sample with sediment during its collection. But Candona truncata was represented by considerably higher percentages (up to 21%) and was present more consistently (in 60% of the samples), suggesting that this species was actually living in the low-plant samples. These data lead to the suggestion that some typically benthic ostracod species are able to creep over low vegetation, especially over densely matted vegetation, as in some of the Elk Lake samples, despite their poor swimming abilities.

2. Benthic Ostracod Community

All sediment samples of Elk Lake (Table 7) were included in

the benthic ostracod community when the data were examined with the 50% rule. The unity of the community is confirmed by the occurrence of Candona ohioensis as one of the dominant species throughout most of the community. Within the benthic community, five subcommunities were recognized on the basis of the differences in predominant species and member species. The subcommunities, which were found to correspond quite closely with habitat variations, were named by the dominant feature of the habitat associated with each subcommunity.

As discussed above, the recognition of a clearly defined ostracod community associated with bare sediment is opposed to the view of Hoff (1942). Hoff found that "Candona biangulata appears to be the only ostracod found in the majority of instances on bare bottom". As discussed above, Hoff's conclusion that ostracods exhibit little habitat specificity within the littoral zone is probably the result of his use of frequency data rather than relative species abundance. The sediment samples of Elk Lake contain low numbers of typical plant-associated species, and frequency data would not indicate as clearly the predominance of benthic species. Hoff also concluded from his studies that "in regard to the effect of the type of bottom on the occurrence of ostracods no very definite correlation has been found in most species, and the distribution appears usually to be random as far as the type of bottom is concerned". However, his comparative data included actively swimming species, which would not be expected to live in the sediment so probably would not be limited by the nature of the sediments. When only creeping and burrowing species are considered, his results do indicate a correlation between ostracod occurrence and type of bottom. He found that

many of the Candona species, which are typically benthic in habitat, "show a slight correlation with the type of bottom, a more-than average number of collections being made on a mud bottom for many of the species". The present study in Elk Lake confirms that sediment type has a definite effect on the distribution of creeping and burrowing ostracod species.

In the present study, the benthic ostracod community probably includes ostracods burrowing in the sediment, crawling on the sediment, and swimming very close to the sediment surface. The sampling technique was not designed to separate species occurring in these habitats, but differences in the locomotory apparatus of the sediment-associated species suggests that species may exhibit such preferences. Physocypria pustulosa and the two Cypria species have well-developed swimming setae (Hoff, 1942) and probably spend a considerable part of their time swimming above the sediment surface. All three of these species were identified in the live trap collections (Table 11), confirming their active swimming abilities. On the other hand, Darwinula stevensoni and the Candona species have no swimming setae (Hoff, 1942) and are consequently limited to burrowing in the sediment or crawling on the sediment surface or in dense vegetation mats, as discussed above. These differences in habitat must be taken into consideration when attempts are made to correlate sediment-associated species with sediment types, because species that live on or just above the sediment surface may not be affected by differences in sediment texture.

a) Nearshore sand subcommunity (0-1 m water depth)

i) Species composition

The dominant species of this subcommunity are Physocypria pus-
tulosa and Darwinula stevensoni. The plant-associated species, Cy-
pridopsis vidua and Cyclocypris sp., are represented, as well as
the typically benthic Candona ohioensis, C. acuta, and C. candida.
The absence of both Cypria species is also an important feature of
the species composition of the subcommunity.

ii) Habitat factors controlling species composition

The nature of the sediment, consisting of almost pure sand, is
doubtless the most important habitat feature limiting the distribu-
tion of this subcommunity. The Candona species seem to be poorly re-
presented in this habitat, compared to the adjacent subcommunity on
soft mud sediments. Hoff (1942) also found that many of the Candona
species were more abundant on mud bottom than on sand, since "most
of the Candoninae crawl on the bottom, and mud is more favorable
for animals of such a habitat than is a sand bottom". Cole (1955),
in his studies of Lake Itasca and Crystal Lake, found that Candona
species were found in the littoral zone only in plant sapropel, not
on firmly packed sand or on marl. The complete absence of both
Cypria species in all sand samples in the present study also seems
to demonstrate the strong controlling effect of the nature of sedi-
ment on benthic ostracods. Perhaps the sediment type influences the
distribution of Cypria species through the food preferences of
these animals. In a study in Coon Lake, Anoka County, Swain (1957)
found a species of Cypria to be twice as abundant in the deep water
as in the shallow water. He attributes the sediment preference of
this species to the greater availability of its food source in the
gyttja of the deeper waters than in the sandy sediment near the

shore.

Whereas some ostracod species are apparently limited by the sandy substrate in the shallow waters of Elk Lake, other species seem to exhibit greater abundance in this subcommunity. Darwinula stevensoni has considerably higher populations in the sandy near-shore sediments than in the adjacent soft mud. But this species probably does not respond simply to this difference in the texture of sediment, for it is also abundant in soft sediments of deeper waters (5-6 m). The distribution of this species may be controlled by the density of vegetation, for it is found in the sparsely vegetated nearshore sand zone as well as in the deeper waters beyond the littoral vegetation zone. This conclusion is strengthened by other records of this species on sandy sediments (Hoff, 1942; Moore, 1939) and on mud bottoms at considerable depths (Furtos, 1933).

The abundance of Physocypria pustulosa in the nearshore sand zone may be the result of a more direct influence of the sediment texture. Perhaps this species, being an active swimmer, can live better in sand, for it can move freely in the spaces between the sand grains. Or perhaps the species lives mainly above the sediment surface and is therefore not limited by the nature of the sediment. The occurrence of this species as an important component of the plant-associated community in the very shallow water samples (30 cm) suggests that many individuals were swimming above the sediment surface; this may account for the high numbers of it in the nearshore sand subcommunity.

Cypridopsis vidua and Cyclocypris sp., normally associated with aquatic plants rather than with sediment in the Elk Lake study, also

seem to be quite well represented in the sediment samples in the nearshore sand subcommunity. They may be able to move in the spaces between the sand grains, as suggested for Physocypria pustulosa.

b) Dense-vegetation subcommunity (1-4 m water depth)

i) Species composition

The dominant species of this subcommunity are Physocypria pustulosa, Candona acuta, and C. ohioensis. Member species include two species of Cypria (C. turneri and C. sp.) and five other species of Candona, the most abundant being C. truncata and C. candida. The plant-associated species, Cypridopsis vidua and Cyclocypris sp., are poorly represented.

Some of the species represented in the dense-vegetation subcommunity are almost restricted to this zone (some Candona species), whereas some extend their range into deep water in smaller abundance (Physocypria pustulosa and Cypria sp.), and others show little difference in abundance in deeper water (Cypria turneri and Candona ohioensis), and still others become more abundant in deep waters (Candona decora).

ii) Habitat factors controlling species composition

Several ecological factors possibly determining the lower limit of this subcommunity may be suggested:

1) Association with aquatic plants

Several ostracod species seem to exhibit a preference for the zone of dense aquatic plants. The plant-associated species, Cypridopsis vidua, although poorly represented in the sediment samples, seems to be more abundant in this zone than in the sparse vegetation zone of deeper water, as expected due to its association with

aquatic plants. Several other species, although probably strictly benthic in habitat, seem to be largely restricted to the littoral zone of Elk Lake, especially to the zone of dense vegetation. These species include Candona acuta, C. truncata, C. candida, C. distincta, and C. elliptica. Ecological notes recorded by other authors also suggest an association of these species with aquatic vegetation. Hoff (1942) made most of his collections of Candona acuta in "grass and decaying vegetation along the edges of small streams". Furtos (1933) reports Candona elliptica as living "on muddy weedy bottoms of permanent bodies of water". C. distincta was collected by Hoff from "a small temporary prairie pond and a grassy roadside ditch". Furtos (1933) describes the occurrence of Candona truncata as "common in temporary and permanent ponds and marshes". Evidence of association of some of these species with aquatic plants is also found in the Pleistocene samples collected and studied by Staplin (1963a). He reported that Candona acuta, C. truncata, and C. candida were always found in association with vegetation remains.

If the above-mentioned species are truly restricted to habitats in which aquatic plants are present, it may be suggested that their distribution is controlled by a food preference for aquatic plants. Although most ostracods are filter-feeders, some are able to eat decaying plant material (Hoff, 1942) and perhaps living plants (Swain, 1957). In a study carried out in Coon Lake, Anoka County, most of the ostracods were found in the pondweed rather than in the sediment, and the assumption was made that they were feeding directly on the pondweed (Swain, 1957).

Although the above evidence suggests that some ostracod

species may be restricted to the littoral zone, perhaps by a food preference, other evidence derived from the present study seems to contradict such a conclusion. Several of these species, Candona acuta, C. candida, and C. distincta, apparently lived in considerable abundance in the deep waters of Elk Lake in earlier postglacial times. The depth of occurrence of the fossil ostracod valves in the Elk Lake cores and the low numbers of seeds of aquatic plants found associated with the ostracods suggests that these species lived in water too deep to permit growth of aquatic plants. This evidence suggests that some factor other than the extent of aquatic vegetation may limit these species to shallow water in Elk Lake at present.

2) Light

Light may be a factor that limits the depth distribution of ostracods. Ward and Whipple (1918) state that light affects the local distribution of ostracods that actively swim or clamber over the substrate. These forms are more abundant in the sunnier areas of a pool than in shaded areas, for they are positively heliotropic. But light probably has little or no effect on burrowing forms, which often live in the deeper, darker areas. This factor may therefore be unimportant in the depth distribution of the benthic ostracods of the littoral zone.

3) Water movement

In his studies in Illinois, Hoff (1942) found that velocity of water flow has a definite effect on ostracod distribution. He considered velocity to be the most important factor in freshwater ostracod ecology and stated that "in general, the more common species

are limited in their habitat range only by the generalized conditions expressed in still temporary waters, permanent still waters, temporary running waters and permanent running waters or by much finer analysis of environmental conditions than has been possible in field studies". In the present study, it may be suggested that the ostracod species, which are restricted mainly to the dense vegetation, respond to the water currents that are effective in this zone. Evidence of water movements, presumably backwater currents resulting from wave activity, is found in the morphology of the marl terrace. The currents seem to decline at about 4 m water depth where the terrace falls off. This corresponds well with the occurrence of littoral ostracods, which begin to decrease quite abruptly at this depth. Perhaps these ostracods, being filter-feeders, require water movements to provide a continuous supply of food. Staplin (1963a) suggests that current may be important through its effect on the oxygen content of the water, as discussed earlier.

4) Sediment type

Another factor possibly influencing the distribution of ostracods in the dense vegetation subcommunity is sediment type. In Elk Lake the sediments of the terrace consist generally of light brown marl with considerable quantities of mollusc shells, pieces of calcite, plant fragments, Rivularia fossils, and chironomid-case remains. Beyond a depth of 3.7 m, the sediment is a fine black gyttja containing few large particles other than chironomid-case remains. Perhaps the decline in typical dense-vegetation ostracods at this depth is a response to this marked change in the nature of the sediments. The ostracods may be affected either by

the chemical nature of the sediment, which is presumably more calcareous on the terrace, or by the texture of the sediment, which is much coarser on the terrace.

c) Sparse-vegetation subcommunity (4-6 m water depth)

i) Species composition

The dominant species of this zone are Darwinula stvensoni and Candona ohioensis. Several other species are represented by low numbers of individuals (Table 7).

ii) Habitat factors controlling species composition

The environmental factors which may be responsible for determining the lower limit of this zone may be:

1) Oxygen

There seems to be evidence, at least in the case of Candona acuta, that oxygen content of the water may be a factor limiting some ostracods to the littoral zone of Elk Lake. This species apparently lived on the ridge (12 m water depth) of Elk Lake until fairly recent times, according to the fossil evidence recorded in the Elk 69-5 core. Perhaps this species was eliminated from the deep waters of Elk Lake when the water level of the lake was raised by about one meter by the construction of a dam in 1917. The fertilization of the lake by the inwash of soil probably lowered the oxygen content of deep waters, and thus limited the occurrence of C. acuta to shallower waters, eliminating the ridge population. This suggestion that the oxygen content of lake waters influences the depth distribution of Candona acuta seems to be supported by a comparison between depth distributions of this species in Elk Lake and in Green Lake (Tables 7 and 9). Green Lake, which has much higher

oxygen content in deep waters than Elk Lake (Table 10 and Fig. 11), shows considerably deeper occurrence of this species than Elk Lake.

The lower limit of the sparse-vegetation subcommunity seems to correspond to the beginning of oxygen decline at about 6 m (Fig. 11). This strongly suggests that oxygen content of lake waters are limiting the distribution of littoral ostracod species.

3) Temperature

Staplin (1963a) suggests that depth distribution of ostracods may be largely due to temperature tolerances of species, as is the case with marine ostracods. In general, marine ostracods tend to occur at the depth that corresponds to their optimum temperature, especially during the breeding season. Also, shallow-water species of the North Atlantic are found in much deeper water in warmer latitudes. But little data on depth distribution of ostracods in relation to temperature are available for freshwater ostracods, and Staplin suggests that the generalization for marine ostracods may not be valid for freshwater ostracods. There is, however, some evidence that temperature may also be an important limiting factor for freshwater ostracods. Staplin (1963a) has observed that species characteristic of warmer waters are the same as those that occur in shallow water. Furtos (1933) suggests that the seasonal succession of ostracod species may be a response to changes in water temperature. Some species of ostracods were found by Staplin (1963a) to be valuable as temperature indicators in Pleistocene deposits in Illinois, for cold-hardy species living today in cooler lakes were found in deposits that were laid down in front of Tazewell ice, in cool lakes of the Illinoian and Wisconsin glacial ages, and in

post-Valders varved clay of the Lake Michigan basin.

In the present study, there is some evidence that temperature may limit the distribution of benthic ostracods in the littoral zone. The ostracod fauna of the littoral zone in winter was examined by the collection of a sediment sample at a water depth of 2 m on November 29, 1969, when the lake was covered by a layer of ice approximately 4 inches thick. In the 45 cc sample of sediment examined, the following live species were noted:

| | |
|------------------------------|----|
| <u>Cypridopsis vidua</u> | 1 |
| <u>Cyclocypris</u> sp. | 2 |
| <u>Candona decora</u> (?) | 1 |
| <u>C. albicans</u> | 6 |
| <u>Physocypris pustulosa</u> | 15 |

These data indicate that all of the Candona species typical of the warm littoral waters in summer are apparently absent (but data may be incomplete) whereas a different species of Candona, C. albicans, is quite abundant. Other species, Candona decora and Physocypris pustulosa, which are able to extend their range into the cooler profundal waters in summer, remain active under the cold-water conditions of winter. But Candona ohioensis and Cypria turneri, which are the dominant species of the profundal zone in summer, are absent in this winter sample, leaving doubt whether cold-temperature tolerance is actually an important factor in the summer depth distribution of ostracods. However, the lower limit of the sparse-vegetation subcommunity may be related to the very abrupt temperature decline observed in Elk Lake at 7 m water depth at the time of the study (Fig. 11), suggesting that temperature is a limiting factor.

d) Sublittoral-profundal subcommunity (6-12.5 m water depth)

i) Species composition

The predominant species of this subcommunity are Candona ohioensis and Cypria turneri. Two other species, Candona decora and Physocypria pustulosa, are represented in several samples. Cypria sp., Candona acuta, and Cyclocypris sp. are each found in only one sample. As discussed above, Cyclocypris is usually plant-associated but may occasionally be carried into deep water as adventitious plankton.

ii) Habitat factors controlling species composition

The oxygen content of the water is probably the main factor controlling the depth distribution of this subcommunity. Most of the community lies within the profundal zone of Elk Lake, which presumably began at about 7.5 m water depth at the time of the study in June, 1969 (Fig. 11). A very sharp thermocline was observed between 7.0 m and 7.5 m, and oxygen content of the water probably declined rapidly in the same interval. Oxygen measurements carried out by the Winkler technique revealed a decline from 9.3 ppm to 5.9 ppm between the 6.0-6.5 m sample and the 8.0-8.5 m sample. This seems to represent the usual oxygen stratification for Elk Lake at this season for it corresponds quite closely with the data recorded by A. L. Baker during the summer of 1967 (Fig. 5 and 11) and by R. O. Megard in July of 1965 and 1966 (Fig. 11). Their data show the rapid oxygen decline, which presumably corresponds to the thermocline, occurring at a depth of about 8-10 m throughout most of the summer.

No oxygen measurements were made below a depth of 9 m in the

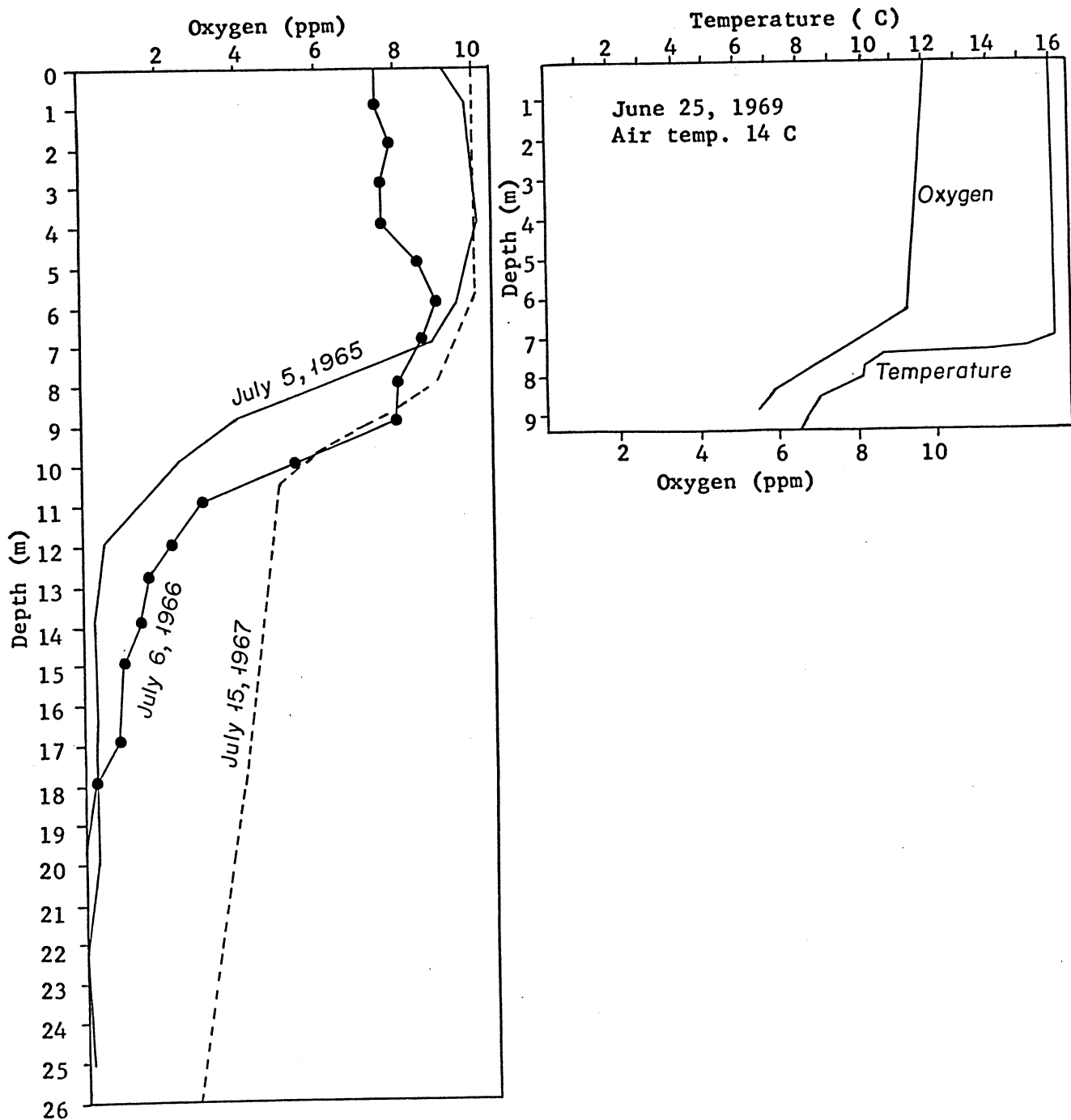


Fig. 11. Stratification of Elk Lake in 1965, 1966, 1967 and 1969.
Data for 1965 and 1966 from R. O. Megard; for 1967 from A. L. Baker.

present study, but presumably the lower limits of this subcommunity at about 12.5 m is limited by very low oxygen content of the water. Figure 11 indicates that oxygen content at this depth was 2 ppm or less in early July of 1965 and 1966. The other ecological factors possibly limiting depth distribution of ostracods (temperature, light, water movements, and sediment type) are probably not important in setting the lower limits of this ostracod subcommunity, for there is probably little change in these factors within the profundal zone.

In view of the description of the habitat, especially with regard to oxygen content of the water, the most significant characteristic of the ostracods of this subcommunity is their ability to survive under low oxygen conditions. However, their tolerance seems to reach a limit in the deep waters of Elk Lake, presumably as the oxygen content of the water reaches a critically low value. It is interesting to note that all of the important species (represented in more than one sample) seem to fall off at approximately the same depth, about 12.5 m, indicating that they have the same lower limit of tolerance to low oxygen.

It is significant to observe that the depth at which the subcommunity declines at the time of sampling of living ostracods (June 13 and 25, 1969) may not represent the extent of the subcommunity at all times. All of these species are represented by considerable numbers of fossil valves in the surface sediments completely across Elk Lake. If these fossil valves represent organisms formerly living in situ and not transported to deep waters, it may be assumed that these species often live in much deeper waters than

observed in the ecological study, perhaps in early spring and late fall and winter when more oxygen is available in deep waters. Evidence that there is probably little transportation of fossil valves in deep water will be discussed in a later section.

The occurrence of ostracods in the low-oxygen profundal zone of Elk Lake is not unexpected in view of other records of ostracods under low oxygen conditions. Cole (1955) identified Cypria turneri and Physocypria pustulosa in the profundal zone of Crystal Lake in Minnesota. Moore (1939) found Cypria exsculpta (synonym of C. turneri) as well as another species of Cypria and two species of Candona in the profundal zone of Douglas Lake, Michigan. Lindeman (1942a), in his experimental simulation of winter anaerobiosis, found that a Candona species in culture did not survive 30 days while a Cypria species was still present after 90 days when the oxygen had fallen very far, but disappeared at 120 days. Pennak (1953) reported that "some species of Candona and Cypris are able to survive long periods of stagnation and oxygen exhaustion on lake bottoms". Ward and Whipple (1918) note that Cypria ophthalmica and Cyclocypris laevis can live for long periods in aquarium water that has not been freshened. These records indicate that some of the species found in the profundal zone of Elk Lake (Cypria turneri and Physocypria pustulosa) have been reported in such habitats, while others, particularly Candona ohioensis and C. decora, seem to have no previous record in profundal habitats. Furtos (1933) and Staplin (1963a) report Candona ohioensis only from vegetated habitats, while Furtos (1933) states that C. decora occurs "in ponds and small lakes".

Although oxygen content of lake waters probably is the most important factor limiting the distribution of ostracods in deep water, it is not certain whether oxygen content of water affects ostracods directly, presumably by its effect on respiration, or whether the effect is indirect. Low oxygen tension of water is usually accompanied by high carbon dioxide content and thus a low pH value, which may affect ostracods through its effect on the carbonate content of water (Staplin, 1963a). Hoff (1942) found that ostracods with large, heavily calcified shells, as the Candona species, do not tolerate acid conditions, whereas species with shells protected by a heavy organic covering, as the Cypria species, Physocypria pustulosa, and Cypridopsis vidua, are able to tolerate acid conditions. Hoff used this information to explain the distribution of some ostracod species in Illinois, for the waters of the southern part of the state tend to be more acid in nature than northern waters. That this factor may affect ostracod distributions within a lake is demonstrated in a study in Coon Lake, Anoka County, where ostracods in shallow water had well-calcified shells, but the Cypria in the deeper waters were poorly calcified (Swain, 1957). In the present study, it was observed that valves of Physocypria pustulosa were heavily calcified in shallow-water samples but very poorly calcified in deeper water.

e) Ridge subcommunity

i) Species composition

Only two species, Candona decora and C. ohioensis, were found living on the ridge (about 12 m water depth) near the middle of Elk Lake. The predominance of these two species is also shown clearly

by the high numbers of fossil valves of these species in surface sediments on the ridge (Plate 4).

ii) Habitat factors controlling species composition

The depth of this subcommunity, about 12 m, would seem to place it in the sublittoral-profundal community discussed above, but its species composition and its apparently very high ostracod population seem to set it apart as a separate subcommunity. Fossil valves of most of the species of the deep waters of Elk Lake (i.e. Cypria spp., Physocypria pustulosa) are found fairly evenly distributed across the basin, but Candona decora and C. ohioensis show very pronounced maxima on the ridge. This fossil distribution may be a result of the differences in modes of locomotion of deep-water species. The Cypria species and Physocypria pustulosa, which have well-developed swimming setae and probably spend at least part of their time swimming above the sediment surface, may be carried by bottom currents after death and distributed evenly across the basin, even though they may live in restricted areas, perhaps on the ridge with the Candona species. On the other hand, the two Candona species of the ridge, spending most of their time burrowing in or crawling on the sediments, probably die beneath the sediment surface and are not transported by bottom currents. Despite this reasoning, which may discount the fossil evidence of a unique ostracod community on the ridge, the study of living ostracods in Elk Lake points to the same conclusion — a maximum of both Candona species, but especially of Candona decora, on the ridge, with no other ostracod species present (but absence of other profundal ostracods may be the result of inadequate sampling). The ecological factors producing

this interesting subcommunity on the ridge, at depths equivalent to the normal sublittoral-profundal zone subcommunity, are unknown.

Green Lake

Benthic Ostracod Community

In Green Lake, the survey of ostracod ecology was made by the collection of surface sediment samples, and no study of the ostracod community associated with aquatic plants was made. Hence only the benthic ostracod community is described for this lake. Two subcommunities were recognized within this community, a littoral subcommunity and a sublittoral-(profundal) subcommunity.

a) Littoral subcommunity (0-8 m water depth)

i) Species composition

The predominant species of the littoral subcommunity are Physocypria pustulosa, Candona candida, and C. acuta, with several other species occurring in lower numbers — Candona elliptica, C. albicans, C. ohioensis, Cypria turneri, C. sp., and Cypridopsis vidua.

ii) Habitat factors controlling species composition

The littoral subcommunity in Green Lake presumably extends from the shore to a depth of about 8 m and includes the ridge sample (about 1 m water depth). These depth limits were set mainly on the basis of the distribution of Candona candida and C. elliptica, which are confined to the littoral zone of Elk Lake. No survey of aquatic vegetation, which is very sparse, was made in Green Lake to confirm this presumed extent of the littoral zone, but the sediment sample collected at 8 m water depth contains Chara sp. It is not surprising that the littoral zone of Green Lake extends to greater depths than that of Elk Lake, because the greater transparency of

Green Lake waters allows deeper penetration of light. The sediment of the littoral zone in Green Lake is composed largely of coarse sand and gravel.

As discussed for Elk Lake, the ecological factors limiting the depth distribution of littoral ostracods is uncertain. The plant-associated species, Cypridopsis vidua, which is restricted to a depth of 3.5 m and less, is probably limited by the abundance of aquatic plants. The factors possibly limiting the depth distribution of benthic ostracods of the littoral zone, as discussed for Elk Lake, may be the association with aquatic vegetation, oxygen content of the water, water temperature, light, water movement, and sediment type.

b) Sublittoral-(profundal) subcommunity (8-35 m:water depth)

i) Species composition

The dominant species of this subcommunity are Cypria turneri and Physocypria pustulosa. In addition, Candona ohioensis, C. acuta, and Cypria sp. are present but are less frequent.

ii) Habitat factors controlling species composition

The sublittoral-(profundal) subcommunity extends from about 8 m water depth to the maximum depth of the lake, about 35 m. On June 24, 1969, when surface sediment samples were collected from Green Lake, no stratification of the lake could be detected by temperature and oxygen profiles (Table 10), and therefore no true profundal zone existed in the lake at that time. Very little temperature change was observed from the surface to 30 m (from 17°C to 16.1°C). Oxygen declined from 8.8 ppm at the surface to 8.4 ppm at a depth of 25 m. The lack of stratification in the lake at the time

of observation may have reflected the very strong winds prevailing at that time. Evidence that thermal and oxygen stratification sometimes exists in Green Lake was obtained in data collected by the Minnesota Division of Game and Fish. A thermocline was reported in late August of a previous year at a depth of 9-12 m from the surface, producing a profundal zone with oxygen content as low as 3.8 ppm. Thus a profundal zone is present at times, perhaps in late summer of every year, but the depth distribution of ostracod species is discussed in relation to temperature and oxygen conditions existing in the lake only at the time of sampling.

The two most abundant species, Cypria turneri and Physocypria pustulosa, have been found in deep waters of several other lakes, including Elk Lake. Candona ohioensis was an important constituent of the deep water community of Elk Lake but had not been reported in such a habitat in the literature examined. Candona acuta was present in the deep waters of Green Lake, unlike the present littoral distribution of this species in Elk Lake. The higher oxygen content of deep waters of Green Lake presumably accounts for its occurrence at greater depths in this lake. Cypria sp., which occurred only in one deep-water sample in Elk Lake, was present in greater numbers in Green Lake, its range extending to the deepest sample collected at 28 m. The occurrence of all of the species in depths much greater than their Elk Lake range seems to support the suggestion that oxygen content of lake water controls distribution of these species. The high oxygen content of the water, apparently extending to the bottom of the lake at the time of sampling, presumably allows these ostracods to live at such depths.

Species Structure of Ostracod Communities of Elk Lake and Green Lake:

1. Dominance and diversity

"A very characteristic and consistent feature of communities is that they contain a comparatively few species that are common (dominants) and a comparatively large number of species that are rare" (Odum, 1963). The validity of this statement for Elk Lake and Green Lake ostracod subcommunities may be ascertained by an examination of Table 12.

| | Subcommunities | Dominant species | Other species | Dominant/Other | Total Diversity |
|------------|------------------------------|------------------|---------------|----------------|-----------------|
| Elk Lake | Tall-plant subcom. | 2 | 1 | 2/1 | 3 |
| | Low-plant subcom. | 2 | 5 | 2/5 | 7 |
| | Nearshore sand subcom. | 2 | 5 | 2/5 | 7 |
| | Dense-vegetation sub. | 3 | 10 | 3/10 | 13 |
| | Sparse-vegetation sub. | 2 | 7 | 2/7 | 9 |
| | Sublittoral-profundal sub. | 2 | 5 | 2/5 | 7 |
| | Ridge subcommunity | 2 | 0 | - | 2 |
| Green Lake | Littoral subcommunity | 3 | 6 | 3/6 | 9 |
| | Sublittoral-(profundal) sub. | 2 | 3 | 2/3 | 5 |

Table 12. Species structure of ostracod communities in Elk Lake and in Green Lake.

a) Ratios — Dominant species/Other species

The ratios between dominant species and other species in the subcommunities studied in Elk Lake and Green Lake generally range from 2/7 to 2/3, with three subcommunities having ratios of 2/5. This seems to confirm the above statement of Odum that there are generally more rare species than dominant species in each

community. However, two of the subcommunities have ratios which indicate a distinct diversion from this "normal" species structure. The tall-plant subcommunity has two species that have both been considered dominant species in this study, although one is found in somewhat greater numbers. Only one individual of another species was found in the entire sampling of this subcommunity. The greater number of dominant species as compared to other species seems to make this subcommunity an exception to the normal community structure. The ridge subcommunity of Elk Lake exhibits only two dominants, differing little in abundance, with no other species present. These data, based on only one sample, may be misleading, for other species are probably present, as indicated by the fossil valves found in surface sediments. The apparent disparity from the "normal" species structure in both of these subcommunities may be simply the result of the fact that they are not complete communities and should not be assessed by this general statement, which applies only to complete communities. However, it is interesting to note that most of the ostracod subcommunities studied do have the species structure of a complete community.

A comparison of ratios between the two lakes studied indicates that the ratios in Green Lake are generally higher, for fewer rare species are present. Comparing the ratios of different zones within the lakes reveals that lower ratios are found in the vegetated zones of the lakes, for more rare species are present than in unvegetated zones.

b) Dominance

i) Numbers of dominant species

It is interesting to note that the number of dominant species seems to remain almost the same in all of the subcommunities recognized in both Elk Lake and Green Lake. Two dominant species are found in all subcommunities except the dense-vegetation subcommunity of Elk Lake and the littoral subcommunity of Green Lake, in which three dominant species are found. The greater number of dominant species in the vegetated zones of the lakes indicates that this is the preferred habitat of most ostracods, which is a well-known fact for freshwater ostracods.

Although the number of dominant species in each subcommunity remains almost the same, a comparison between Elk Lake and Green Lake reveals that there are more subcommunities in Elk Lake (but the lower number of subcommunities recognized in Green Lake may be the result of incomplete sampling). The total number of species that are dominant in at least one of the subcommunities of the benthic ostracod community of Elk Lake is six, whereas only four are present in this community in Green Lake. Thus, it seems that the total number of dominant species within a body of water reflects the degree of differentiation of the habitat, which produces conditions suitable for different species to dominate in different parts of the lake.

ii) Kinds of dominant species

Although the number of dominant species remains almost the same in all subcommunities in both Elk Lake and Green Lake, different species combinations are represented. The differences between the species composition of the subcommunities of each community is less than 50%, as discussed above, since the communities were not

delimited by the 50% rule. The comparison between the dominant species of Elk Lake and Green Lake sediment communities illustrates the wide geographical ranges of ostracod species. In the littoral zones of both lakes, Physocypria pustulosa and Candona acuta are among the dominant species, while in the sublittoral-profundal zones of both, Cypria turneri is one of the dominant species. Most of the other dominant species of each lake are found in the other lake as well but in lower numbers so are not included as dominant species.

c) Diversity

The diversity of a community is most easily expressed by the total number of species present. It is an ecological fact that the total number of species is reduced where conditions of existence are severe (Odum, 1963). This is illustrated by a comparison between the diversity of the benthic ostracod community of Elk Lake and that of Green Lake. In Elk Lake, 14 ostracod species have been identified in the collections of live forms and 19 among the fossils or surface sediments, while in Green Lake only 9 species were found living in the lake, although sampling may have been inadequate. The higher number of species in Elk Lake may be due in part to the greater diversity of habitats, but even within subcommunities the number of species was higher in Elk Lake than in Green Lake. One environmental factor possibly favoring ostracod diversity in Elk Lake may be food, since Elk Lake is probably more productive in plankton than Green Lake. This would provide a good supply of fresh organic debris, which is probably the main food of most ostracods (Swain, 1955). The much greater production of aquatic macrophytes,

which also may be an important food source, may also be a factor in the greater diversity of ostracods in Elk Lake. The fine sediment texture of Elk Lake, compared to the coarse sands and gravels of the littoral zone of Green Lake, may also be a significant factor determining the difference in ostracod diversity between the two lakes.

3. Distribution of fossil ostracods in surface sediments

In order to interpret the presence of a certain fossil in a core, it is necessary to know whether the organism actually lived in situ or whether it was transported to this location and deposited subsequent to its death. This is especially important in the present study, because an attempt will be made to estimate past water levels on the basis of the occurrence of fossils at certain depths in the cores. Thus the studies described above were designed to determine the extent to which organisms are transported from their living habitat, either while living or after death. These studies yield some interesting information concerning the redistribution of ostracod fossils in Elk Lake.

There is very little information available in the literature concerning the transportation of fossil ostracods within lakes. Goulden (1964) reported that mandibles of ostracods were quite abundant in the late-glacial and early post-glacial sediments of Esthwaite Water. Frey (1964) suggests that these mandibles, because of their small size, had been transported offshore from the littoral zone where most of the species occur. But the present study deals with fossil ostracod valves, and very little is known concerning their transportation other than the occasional occurrence of

ostracods as adventitious planktonts (Hoff, 1942), suggesting that surface water movements occasionally transport living ostracods from their normal habitat and presumably allow them to be deposited and preserved in sediments far from their original habitat.

The trap studies in Elk Lake should contribute to an understanding of the transportation of fossil ostracod valves within the lake (Table 11). If dead organisms are being carried by water movements, they may be collected in traps placed one meter above the sediment. The samples were collected in alcohol, so all ostracods were dead when the samples were examined, but the freshness of the color of the ostracods suggested that they were recently living and probably represent adventitious plankton rather than transported dead ostracods. This information seems to suggest that there is little transportation of fossil ostracods in waters a meter or more above the sediment surface but does not discount possible movements of fossils at or close to the sediment surface.

The best method of studying the transportation of fossil ostracods within Elk Lake is to compare the lateral distribution of fossil ostracods in the surface sediments with the distribution of living ostracods within the lake. If fossil and living forms have the same distribution, one may assume that no redistribution has taken place, but if the distributions differ, transportation of ostracods is indicated. The distribution of each fossil species identified has been graphed (Plate 4), and species have been grouped according to their patterns of distribution into six types of depth distribution. The distinguishing features of each of these assemblages are:

- 1) Cypria turneri assemblage

This category includes Cypria turneri and C. sp. Fossils of these species are distributed more or less evenly across the basin, with a slight increase in abundance near each shore.

2) Physocypria pustulosa assemblage

This category includes Physocypria pustulosa, Cypridopsis vidua, and Cyclocypris sp. Fossils are distributed across the basin with distinct maxima in the shell zone near each shore.

3) Candona ohioensis assemblage

This category includes C. decora and C. ohioensis. Fossils are distributed across most of the basin, with distinct maxima near the shore and on the ridge.

4) Candona truncata assemblage

This category includes C. candida, C. eriensis, C. distincta, C. punctata, C. elliptica, C. albicans, C. truncata, and C. acuta. Fossils are almost completely limited to single shoreward maxima but with scattered occurrences across the basin.

5) Darwinula stevensoni assemblage

This category includes only Darwinula stevensoni and Potamocypris smaragdina. Fossils are limited to the nearshore zone but with two maxima, one in very shallow water (0.5 m) and the other in the deepest part of the littoral zone.

6) Limnocythere sancti-patricii assemblage

This category includes L. sancti-patricii and L. reticulata. Fossils are almost limited to the nearshore zone, with maxima in the lower littoral zone, but with scattered occurrences across the basin.

Comparison between the fossil and living distributions of

ostracod species in Elk Lake yields the following suggestions concerning transportation of ostracods from their normal living habitat:

1) Some fossil ostracods in deep-water sediments lived in situ. The fossil and living distributions of some ostracod species correspond in deep-water sediments, suggesting that the fossil ostracods lived in situ. Candona ohioensis and C. decora and possibly Cypria turneri and Physocypria pustulosa seem to fall into this category.

Since the Candona species are strictly benthic, they probably die in their normal living habitat beneath the sediment surface and are thus protected from movement by water currents that may exist at or near the sediment surface. Even without such protection, as may be the case for Cypria turneri and Physocypria pustulosa, which probably spend more time above the sediment surface, there would probably be little transportation of fossil ostracods by bottom currents in deep waters. Mueller (1964), in his studies of the distribution of cladoceran remains in the surficial sediments of three northern Indiana lakes, found that the magnitude of the transporting agent diminishes at depths below the metalimnion.

2) Some fossil ostracods in deep-water sediments are probably transported to this location by water movements in the epilimnion. Some ostracods were found as fossils in deep-water sediments, but few or no living individuals were found in the sediment at such depths. Cypridopsis vidua and Cyclocypris sp. seem to fall into this category. These species were the dominant ostracods found on plants and in live traps, suggesting that they are active swimmers and thus capable of entering the plankton occasionally as adventitious

planktonts. Another factor favoring their transportation into deep water is the location of their habitat. Since these species seem to live habitually in the upper levels of the epilimnion near shore, they are probably easily carried out to deeper areas by the water currents of the epilimnion.

3) Most fossil ostracods in shallow-water sediments were transported by water movements and deposited in the shell zone. Most fossil ostracods found in shallow water exhibit a maximum in the shell zone, especially in the 3.3-m sample at the northern end of the lake and the 10-m sample at the southern end. Since the living ostracods are more evenly distributed within the littoral zone, the assumption has been made that fossil ostracods are concentrated in the shell zone by backwater currents, as discussed in the section dealing with the formation of the terrace and shell zone in Elk Lake. Fossil ostracods reach their maximum at the same depth as fossil molluscs, but their distribution extends more deeply than that of molluscs, suggesting that offshore currents carry the smallest and lightest fossil remains farthest.

Although these assumptions concerning transport of fossil ostracods in Elk Lake are useful in the interpretation of the stratigraphic ostracod studies in Elk Lake, the present movement pattern of fossils may be quite different from that of the past. For instance, the formation of the terrace in Elk Lake began only at the time of the Quercus-Ostrya pollen zone. Before that time, the transportation pattern of fossils in shallow water may have been different from that of the present pattern described above. Transportation of fossils to deep water may also have been quite different in

the past. At present, Elk Lake is stratified in summer, and the overturns of spring and fall may not be complete (A. L. Baker, personal communication). If in the past the lake circulated more often and more completely, there would probably have been considerably more movement of shallow-water ostracod fossils into deep waters.

4. Ostracod stratigraphy

The few stratigraphic studies of ostracods that have been carried out are reviewed by Frey (1964), who summarizes the interpretations of past environmental conditions based on ostracod stratigraphies. Changes in ostracod species in cores have been variously interpreted as reflections of changing environmental conditions (pond, stream, peat, and lake phases), changes in chlorinity of waters, changes in climate, and competition among ostracod species. Few of the early works were quantitative stratigraphic studies of individual species, but recently such a study has been carried out by Klassen et al. (1967) on the Roaring River Clay, a Pleistocene deposit in southwestern Manitoba. The present study of ostracod stratigraphy in several Elk Lake cores is also based on quantitative studies of individual species, and the results are indicated in Plates 6-11 and 13.

The interpretation of past limnological conditions in Elk Lake on the basis of the ostracod stratigraphy of Elk Lake cores is hindered by the lack of ecological information available for the ostracod species represented in the cores. The interpretations will be made largely on the basis of the ecological studies of ostracods carried out in the present study, and the interpretations are supported by the paleolimnological evidence supplied by other fossil

aquatic organisms studied in the same cores, by fossil pollen, and by sediment characteristics. The ostracod stratigraphy of Elk Lake will be discussed with respect to the five units that have been recognized in the Elk Lake cores on the basis of distinctive faunas of ostracods, chironomids, and molluscs, as well as by distinctive sediment types in most cases. Since the stratigraphy of the deep-water cores (C and 69-5) is quite different from that of the shallow-water cores (69-1, 69-2, 69-3, and 69-4), they will be discussed separately.

1) Stratigraphy of deep-water cores 69-5 and C (including also information derived from the two short cores)

The stratigraphy of the deep-water cores seems to indicate that in all units except A, changes in oxygen concentration of Elk Lake waters at these depths was probably the main factor controlling the changes in ostracod populations. The following interpretations of past limnological conditions in the five faunal units of Elk Lake may be suggested:

Unit A - Ostracods were found in unit A only in the 69-5 core. Shells of five ostracod species were found in this unit: Candona swaini, C. caudata, Cytherissa lacustris, Limnocythere reticulata, and Cypricercus reticulatus. All species are represented by low numbers of fossils, especially the last two species listed above. Fossil ostracods are very sparse in the lower 30 cm of the core (1630-1600 cm), enter in fair numbers at about 1600 cm, and show a slight increase in abundance towards the top of the unit.

Although only one of these species is represented in Elk Lake at present, considerable ecological information concerning some of

the species is available in a study of the Pleistocene ostracods carried out by Staplin (1963a, 1963b). Candona swaini and C. caudata are both common in the late Pleistocene terrace silts, lake clays, and silts of Illinois and in the Lake Illinois delta sands (Staplin, 1963a). Candona swaini, which was extremely abundant in the Pleistocene deposits of Illinois, was one of the only two species found in Tazewell deposits formed by ice-damming and is often associated with cold-water stenothermic species in other Pleistocene deposits. The occurrence of these two cold-hardy species in unit A of Elk Lake suggests Pleistocene environmental conditions similar to those in which these species were found in Illinois, and the hypothesis that unit A sediments in Elk Lake represent outwash from the nearby St. Louis sublobe (probably redeposited by erosion) may support this suggestion. Although these species can tolerate such conditions, they are not restricted to such environments. Candona caudata is a common species in central and northern Europe at present (Hoff, 1942), and C. swaini, although found only in Lake St. John in Colorado at present (Staplin, 1963a), was quite abundant in Elk Lake sediments until the top of the Quercus-Gramineae-Artemisia pollen zone. The other species found in unit A probably have the same temperature tolerances, being capable of withstanding rigorous climates but also being found in milder climates. Cypricercus reticulatus was also identified in the Pleistocene deposits of Illinois (Staplin, 1963a) and has been described in the Arctic region of North America, but it is also common throughout the Holarctic region (Hoff, 1942). Cytherissa lacustris and Limnocythere reticulata, both found in the Pleistocene deposits of Illinois, occur today in

temperate regions (Staplin, 1963b).

The low numbers of fossil ostracods per unit volume of sediment in unit A may be the result of several factors. The rapid rate of sedimentation, which probably resulted from the abundance of clastic materials carried into Elk Lake at this time, would result in low numbers of fossil organisms per unit volume of sediment even if populations were fairly high. However, the turbidity of Elk Lake waters during this period, suggested by the considerable quantities of fine silt deposited in the 69-5 core, along with the low temperature that presumably prevailed, probably prevented high productivity of algal populations, so the productivity of the animal communities of the lake was doubtless also low.

Unit B - This unit is characterized by high values of Candona candida, C. ohioensis, and Cytherissa lacustris in both the 69-5 and C cores and of Candona sp. and Limnocythere reticulata in core C. Several other species are represented in this zone in relatively low numbers. The ostracod community that lived in Elk Lake at the depths represented by these cores (14-16 m) suggests oligotrophic or mesotrophic lake conditions, with fairly high oxygen content of lake waters, as was suggested by the chironomid and mollusc fossils in zone B. Candona candida seems to require high oxygen, because it is one of the ostracods limited to shallow waters in both Elk Lake and Green Lake, as shown in the ecological studies discussed above. All Pleistocene specimens of this species were taken from silts deposited in still, relatively shallow waters (Staplin, 1963a). Cytherissa lacustris also seems to require waters of fairly high oxygen content, being characteristic of deep waters of oligotrophic lakes. Staplin (1963b) states that "although it has been reported from the

littoral zone of the lakes, it is most common at fairly great depths in cold water. In Sweden, it is common in the larger lakes and some of the mountain lakes". Klassen et al. (1967) found this species to be the most abundant ostracod in the oligotrophic phases represented in the Roaring River Clay, a Pleistocene deposit in southwestern Manitoba.

Unit C - This unit is characterized by maxima in Candona ohioensis, C. decora, C. swaini, and Limnocythere reticulata in both the 69-5 and C cores, with lesser maxima in C. distincta and Cypria sp. The species C. candida and Cytherissa lacustris, which reached their maxima in the preceding unit, maintained themselves in considerable abundance in this unit. Several other species occur in very low numbers. The ostracod community represented in this unit suggests lower oxygen conditions in Elk Lake, as do the chironomids and molluscs. Candona ohioensis and C. decora are presumably able to tolerate fairly low oxygen conditions, for these two species are abundant in Elk Lake today at depths that are below the thermocline most of the year. Although Limnocythere reticulata lives in a variety of habitats, Elk Lake studies suggest that this species is favored by fairly low oxygen conditions. In unit E', presumably representing the period since eutrophication of Elk Lake by soil inwash in 1917, this species shows the greatest and most rapid population increase at the beginning of the unit. Although other ecological factors may have influenced the population, it may be suggested that the lowered oxygen conditions, which may have accompanied the pollution, was responsible for the increase in population of this species. Studies of the fossil distribution carried out on the

surface sediments of Elk Lake showed that Limnocythere reticulata has a maximum in deeper water than most littoral ostracods, also suggesting tolerance of lower oxygen conditions. Cypria sp. is also able to tolerate fairly low oxygen conditions, being found living beyond the littoral zone in both Elk Lake and Green Lake. This species, however, is presumably less tolerant of low oxygen than Cypria turneri, since it is not found living as deep as this species in Elk Lake. No information concerning oxygen tolerance of Candona swaini is available.

The very high numbers of ostracod fossils per unit volume of sediment in unit C probably reflects the increased productivity of Elk Lake in this period, although the abundance of fossils may be in part the result of low sedimentation rate at this time, at least in core 69-5. If approximate sedimentation rates are calculated for core 69-5 by transferring C¹⁴ dates of the pollen zone boundaries of nearby Bog D pollen diagram to corresponding pollen zone boundaries in this core, unit C has an average sedimentation rate of 9.6 yrs/cm, in contrast to a rate of 56.8 yrs/cm in the unit below and 30 yrs/cm in the unit above. When these differences in sedimentation rate are taken into consideration, the same species maintain their maxima in this unit, but the maxima are not so distinct.

Unit D - All ostracod species show a very abrupt decline in abundance at the beginning of this unit, and by the end of the unit only Candona ohioensis and C. decora are significantly represented in these two cores. A general decrease in productivity of Elk Lake or a change in some factor critical to ostracod survival at these depths (e. g. decrease in oxygen) may be suggested as possible

explanations for this change in ostracod populations. Lowered oxygen seems to be a good explanation, since the only two species that survive are relatively tolerant of low oxygen conditions. However, the chironomids show little increase, as would be expected if oxygen content was lowered, and diatoms suggest quite high oxygen rather than low oxygen. Therefore a general decrease in productivity of Elk Lake is considered to be the most plausible explanation of the ostracod population decline in this unit.

Unit E - Only three ostracod species are well represented in this unit in cores 69-5 and C. Candona ohioensis and C. decora are still present in considerable abundance. Candona acuta enters core 69-5 for the first time in unit E, although it had been present in core C since the beginning of unit C. The ostracod community represented in this unit suggests fairly low oxygen conditions in Elk Lake, as indicated also by chironomid fossils. As mentioned above, Candona ohioensis and C. decora seem to be able to tolerate fairly low oxygen conditions, as suggested by the ecological studies carried out in Elk Lake and Green Lake. Candona acuta seems to tolerate lower oxygen conditions than most littoral ostracods, being found living at considerably lower depths than these species in Elk Lake and Green Lake. However, C. acuta is presumably not so tolerant of low oxygen conditions as Candona ohioensis and C. decora, for this species is not present in the ostracod community on the ridge today (Plate 4), when oxygen conditions are probably lowered, whereas C. ohioensis and C. decora persist. The recent disappearance of C. acuta from the Elk Lake ridge is not indicated in the 69-5 core, because surface sediments are not represented in this

core, but no living specimens and few fossil valves of this species were found at these depths in the surface sediment studies.

Subunit E' - This subunit is represented in the ostracod stratigraphy of the short core taken at 8 m water depth (Plate 13) and by a few samples from the frozen short core taken from the deepest hole in Elk Lake. E' is delimited by a fairly abrupt color change in the shallow short core (change from olive to black) and by an even more abrupt transition from fine laminations to broad poorly defined bands in the sediments of the frozen core. This abrupt change in sediment characteristics has been interpreted as a reflection of the eutrophication of Elk Lake in 1917 when considerable quantities of soil are believed to have been washed into the lake. This interpretation seems to be supported by chironomid stratigraphy studied in the shallow short core and diatom stratigraphy studied in the frozen short core. It is therefore reasonable to interpret the very marked changes in ostracod stratigraphy that occurred at the same level as a result of eutrophication, even though little information concerning the trophic status of the ostracod species is available.

In the shallow short core, subunit E' is preceded by a layer of about 10 cm thickness in which considerable quantities of mollusc shells occur. The ostracod stratigraphy in this layer seems to be mainly resulting from the deposition of coarse shells. Cypria sp. and Cypria turneri, which presumably require soft sediments (Swain, 1957), decline very markedly in this layer. Some species, such as Candona ohioensis, C. acuta, and C. truncata, increase in this layer, perhaps due to their preference for new habitat conditions,

or perhaps due simply to competition, as these species replace declining Cypria species. The occurrence of fossil valves of Candona swaini and Cytherissa lacustris in this layer suggests redeposition from older sediments, which may have been exposed by the strong currents that presumably existed to carry shell zone deposits to the unusually great depths in this period. Both of these species were abundant in older sediments, but no fossil valves of Cytherissa lacustris and very few valves of Candona swaini had been found in sediments of Elk Lake cores above unit D.

In the shallow-water short core, subunit E' begins with an abrupt increase in abundance of many ostracod species, including Candona ohioensis, C. decora, C. candida, Limnocythere reticulata, Physocypria pustulosa, Cypridopsis vidua, Cyclocypris sp. and Darwinula stevensoni. The most abundant ostracod species in this early period on subunit E' is Limnocythere reticulata. The fact that almost all of the ostracod species in the shallow-water core exhibit a population increase at this time suggests that the abundance of shallow-water ostracods is determined mainly by availability of food. The increase in phytoplankton productivity demonstrated in the diatom stratigraphy is probably the main factor responsible for the population increase of the filter-feeding ostracods. The increase in density of the aquatic macrophyte flora, which probably resulted from the eutrophication of Elk Lake, may have influenced the population increase of Cypridopsis vidua and Cyclocypris sp., which were found to be closely associated with aquatic macrophytes in the ecological study of Elk Lake.

After the initial abrupt increase in populations of many

ostracod species in Elk Lake, a gradual reversion began, and populations of many species returned to approximately normal abundance within 10 cm of the sediment column. The Candona species and Limnocythere reticulata declined as Cypria sp. regained its position as the dominant ostracod. This reversion in the ostracod community was presumably the result of the reversion in the phytoplankton community as the inwash of soil ceased and normal sedimentation buried the soil-containing sediments. However, the lake has not yet completely reverted to pre-disturbance conditions, for dark sediments are still being deposited, and the diatom and chironomid communities have not regained their former species compositions and populations. Ostracods exhibit the same situation — a return to almost normal conditions but with some community changes persisting, especially the maintenance of fairly high populations of Physocypria pustulosa and Cypridopsis vidua. The persistence of high populations of these two species, or at least of the plant-associated species Cypridopsis vidua, may be related to the maintenance of the dense aquatic macrophyte flora that was presumably established at the beginning of subunit E'. Unlike phytoplankton populations that are short-lived and therefore probably reflect environmental changes fairly rapidly, many aquatic macrophytes are propagated by long-lived rhizomes and are therefore more stable in environmental changes.

The few samples examined for ostracod fossils in the frozen short core also seem to indicate a change in ostracod stratigraphy in E'. One sample of 5 cc volume was examined in the finely laminated sediment a short distance below the E' boundary. In this sample only one valve each of Cypridopsis vidua and Physocypria pustulosa

were found. In a sample of 1.5 cc taken 2-5 cm above the E' boundary no ostracods were found. In a sample of 1.5 cc taken 8 cm above the boundary, 2 Cypria turneri, 1 Cypria sp., and 1 Candona truncata were counted. In a sample of 2 cc taken 13 cm above the boundary, 7 Cypria turneri were found. These meagre data seem to suggest that no ostracods lived at this depth immediately after the eutrophication, presumably due to low oxygen, but that a fairly abundant population of Cypria spp. lived at this depth after the initial effects of the pollution had waned, for this ostracod population is different in species composition and abundance from the pre-disturbance community.

2) Stratigraphy of nearshore cores 69-1, 69-2, 69-3, and 69-4

The stratigraphy of the shallow-water cores seems to indicate that changes in the nature of the sediment was the main factor controlling the changes in ostracod population at these depths. The oxygen changes that presumably controlled the ostracod communities in deeper water probably had little effect on shallow-water populations, for oxygen was probably quite high in shallow water throughout the history of the lake.

Unit A is not represented by ostracod fossils in the shallow-water cores, but units B and C are represented in cores 69-2 and 69-3. In these two units, sediments of these two cores change from a sand at the base of unit B to dark gray silt in the upper part of unit B and lower unit C, to a sand in the upper part of unit C. The sandy sediments are dominated by Candona swaini and Ilyocypris gibba, which are known elsewhere to inhabit such a substrate. C. swaini was found in the delta sands of Lake Illinois (Staplin,

1963a), and Ilyocypris is characteristic of running waters (Hoff, 1942), in which sediments are often coarse. Furtos (1933) also records that Ilyocypris gibba is found on "sandy bottoms of large and small lakes". The silty sediments in the lower part of unit C are characterized by Candona decora, C. candida, Physocypris pustulosa, Cypridopsis vidua, and Cyclocypris sp. The occurrence of Candona species in the finer sediments is expected, for these ostracods are burrowing forms typical of soft sediments. The high numbers of the plant-dwelling ostracods in the periods in which finer sediment was deposited may be an indirect effect resulting from the increase in aquatic macrophytes in fine sediment. An increase in Chara spores and of shells of molluscs, which live mainly on aquatic plants, in the zone of fine sediments seems to strengthen this assumption.

In unit D, represented in cores 69-2 and 69-3, a light gray silty copropelic marl was deposited. The much finer nature of the sediments of this unit resulted in an increase in abundance of burrowing Candona species, especially C. ohioensis and C. acuta, and of Limnocythere spp. and Physocypris pustulosa.

Unit E is represented in cores 69-1, 69-2, 69-3, and 69-4. A shell-zone sediment was deposited in this unit in cores 69-2 and 69-3 and in the lower part of this unit in core 69-4. The upper part of this unit in core 69-4, after shell-zone deposition ceased, exhibits considerably higher Cypria populations than the lower part of the unit, probably because Cypria species prefer soft sediments. Swain (1957) found a species of Cypria to be twice as abundant in the gyttja of deeper waters of Coon Lake than in the sandy sediment near the shore. Another significant change in the ostracod

population at the base of unit E is an increase in Cypridopsis vid-
ua and Cyclocypris sp. (cores 69-2 and 69-3). This change is pro-
bably related to the increasing productivity of aquatic macrophytes
at this time rather than to the change in the texture of the sedi-
ments.

DIATOMS

1. Taxonomy

Diatoms represent a class, the Bacillariophyceae, within the algal division Chrysophyta (Smith, 1950). The primary feature distinguishing diatoms from other algae is their highly silicified cell wall, composed of two overlapping halves. The identification of diatoms in the Elk Lake study has been based on the descriptions and illustrations of diatoms included in works by Hustedt (1930) and Patick and Reimer (1966).

2. Ecology

The main ecological factor considered in the interpretations of the Elk Lake cores was the preference of diatom species for certain trophic conditions, i.e. oligotrophic, mesotrophic, and eutrophic conditions. In this respect, ecological information concerning diatom species has been derived not only from various literature sources, but also from the stratigraphic studies of diatoms carried out in short cores from Elk Lake and Sallie Lake, in which changes in diatom species can be related to historical events producing eutrophication of these lakes.

The following ecological information concerning some of the diatom species found in Elk Lake cores has been derived from literature sources:

Asterionella formosa

"Commonly occurs in the plankton of mesotrophic-eutrophic water" (Stockner and Benson, 1967). In Esthwaite Water, an increase in Asterionella formosa in the uppermost sediments was accompanied by a

general increase in species and the appearance of certain indicators of increased eutrophy, and these changes were presumably determined by biotic influence (Round, 1961).

"Eutrophic" (Foged, 1948 in Haworth, 1971).

"In areas of Lake Michigan that have been eutrophied, both the relative abundance and the seasonal dominance of this species are increased" (Stoermer and Yang, 1969).

Cyclotella spp.

"Certain species of the genus Cyclotella are commonly considered oligotrophic indicators" (Rawson, 1956 in Stockner and Benson, 1967).

Cyclotella stelligera

"Eurytopic, occurring in waters of the most different concentration" (Hustedt, 1938a in Florin, 1970).

Cyclotella meneghiniana

"Eutrophic lakes and ponds" (Jorgensen, 1948 in Haworth, 1971).

Fragilaria spp.

"Indicators of increased eutrophy" (Round, 1961).

Fragilaria brevistriata

"Littoral in eutrophic waters" (Foged, 1959 in Haworth, 1971).

Fragilaria capucina var. mesolepta

"Eutrophic" (Jorgensen, 1948 in Haworth, 1971).

Fragilaria construens

"Littoral species of stagnant water" (Jorgensen, 1948 in Haworth, 1971). Most reports in Lake Michigan come from inshore areas that are appreciably eutrophied (Stoermer and Yang, 1969).

Fragilaria crotonensis

"An indicator of eutrophication" (Haworth, 1971).

Fragilaria vaucheriae

"Dominant in...many eutrophic lakes, smaller numbers in ponds"
(Jorgensen, 1948 in Haworth, 1971).

Melosira granulata

"This species is often abundant in eutrophied portions of Lake Michigan" (Stoermer and Yang, 1969).

"Generally an indicator of eutrophication" (Jorgensen, 1948 in Haworth, 1971).

Melosira italica

"Acidiphilous" (Round, 1961).

Stephanodiscus astraea var minutula

Referred to by the alternate name S. minutus in Stoermer and Yang, 1969. They state: "Although S. astraea var minutula has been widely reported, the confusion surrounding this name makes it difficult to determine the actual distribution of the taxon we treat here. In our experience in Lake Michigan, it is a minor component of the off-shore flora and only becomes abundant in estuaries and eutrophied inshore areas of the lake."

"Many eutrophic lakes and ponds" (Jorgensen, 1948 in Haworth, 1971).

Tabellaria fenestrata

"Usually in oligotrophic water, seldom dominant in any other"

(Jarnefelt, 1952 in Haworth, 1971). Holland (1969) found Tabellaria to be one of the major diatoms of Lake Michigan and states that it has been found "associated with oligotrophic waters elsewhere".

This species became abundant in Zürichsee in 1896, two years before the massive growth of Oscillatoria rubescens, suggesting that it may be favored by eutrophic conditions (Stockner and Benson, 1967).

Round (1957) states that Tabellaria species are frequent components of both planktonic and attached communities, but he attributes the large maximum of Tabellaria in the late post-Atlantic period to an increase in attached forms, resulting from the filling and colonization of the basin by higher aquatic plants.

Short core studies:

Considerable ecological information concerning diatom species has been obtained in the short core studies of Elk Lake, Sallie Lake (near Detroit Lakes, Minnesota), and Lake Washington. Table 13 indicates the recent changes in diatom species in the two short cores from Elk Lake, a short core from Sallie Lake (taken at 20 ft water depth in the south basin), and a core from Lake Washington studied by Stockner and Benson (1967). The historical events presumably associated with diatom changes indicated in Table 13 are:

Elk Lake - frozen short core (SCf - Plate 14)

1) Not under the influence of pollution (53-67 cm)

The trophic status of Elk Lake seems to have been mesotrophic before pollution, with Stephanodiscus astraea var minutula as the dominant diatom species and with considerably lower percentage of Fragilaria crotonensis and Asterionella formosa.

2) Under the influence of pollution (0-53 cm)

The event that caused the distinct change in diatom populations, as well as the change in lamination (finely laminated to broadly banded) seems to have been the inwash of considerable quantities of soil due to the raising of the water level by about one meter after the building of a dam at the outlet of Elk Lake at Chambers Creek in 1917 (Dobie, 1959). The extensive lumbering operations

| | Elk Lake (SCf) | Elk Lake (SCs) | Sallie Lake | Lake Washington |
|--|---|--|---|--|
| Not under influence of pollution | <u>Stephanodiscus</u> <u>astraea</u> var <u>minutula</u> (mesotrophic) | | <u>Melosira ital-</u> <u>ica</u> , <u>M. granu-</u> <u>lata</u> (oligotrophic) | <u>Stephanodiscus</u> <u>astraea</u> var <u>minutula</u> , <u>Mel-</u> <u>osira italica</u> (oligotrophic- mesotrophic) |
| | Lamination change | Color change | Color change | |
| Under influence of pollution | a) <u>Fragilaria</u> <u>crotonensis</u> , <u>Asterionella</u> sp., <u>Tabellar-</u> <u>ia fenestrata</u> (eutrophic) | | a) <u>Stephano-</u> <u>discus astraea</u> var <u>minutula</u> (mesotrophic) | <u>Fragilaria</u> <u>crotonensis</u> , <u>F. construens</u> (eutrophic) |
| | b) <u>Stephano-</u> <u>discus astraea</u> var <u>minutula</u> (mesotrophic) | | b) <u>Fragilaria</u> <u>crotonensis</u> , <u>F. capucina</u> var <u>mesolepta</u> , <u>Stephanodiscus</u> <u>astraea</u> var | |
| | c) <u>Melosira</u> <u>italica</u> (mesotrophic- oligotrophic) | <u>Melosira ital-</u> <u>ica</u> , <u>Fragilar-</u> <u>ia</u> spp. | <u>minutula</u> (eutrophic) | |

Table 13. Recent changes in dominant diatom species in Elk Lake, Sallie Lake and Lake Washington. The probable trophic status of the lakes at each stage is indicated.

carried out in the watershed of Elk Lake at this time may also have increased soil inwash by the exposure of forest soils to erosion. Zone (a) (35-53 cm) apparently represents eutrophic conditions under the initial influence of this soil influx, with dominance of Fragilaria crotonensis, Asterionella formosa, and Tabellaria fenestrata. Both Fragilaria crotonensis and Asterionella formosa seem to be reliable indicators of eutrophication, according to the literature sources cited above, but the trophic status of Tabellaria fenestrata seems to be uncertain, some authors suggesting that this species prefers oligotrophic waters and others suggesting that it is favored by eutrophic conditions. The high numbers of this species in the core probably represent planktonic rather than attached

forms, since this species was the most abundant planktonic diatom in Elk Lake on June 24, 1968 (Liisa Koivo, unpub. report).

Zones (b) (25-35 cm) and (c) (0-25 cm) seem to represent stages in reversion of Elk Lake toward normal trophic conditions as soil inwash ceased. Zone (b), represented by a brief dominance of Stephanodiscus astraea var minutula (only one sample in this zone may not be sufficient evidence to recognize the zone), is considered to represent mesotrophic conditions, while in zone (c) the increase in Melosira italica seems to indicate mesotrophic-oligotrophic conditions. These stratigraphic changes in diatom populations were correlated with the brief period of extensive lumbering in the area (1917-1919) (Dobie, 1959) by pollen analysis of the frozen short core, which indicated a quite marked decrease in Pinus pollen at this level (about 53 cm).

Elk Lake - shallow short core (SCs)

1) Not under the influence of pollution (22.5-45 cm)

Almost no diatoms were preserved in this portion of the core, presumably due to the alkalinity of Elk Lake at this time, as is discussed under the section concerning stratigraphy.

2) Under influence of pollution (0-22.5 cm)

No diatoms were preserved in the lower part of this zone, but the zone is delimited by the distinct color change of the sediments at 22.5 cm depth, and by correlation with the frozen short core by pollen analysis. The lack of preservation in the lower part of the zone is unexpected, since the eutrophic conditions of Elk Lake at this time, indicated in the frozen short core, would presumably have lowered the pH sufficiently to allow preservation of diatom

frustules in all parts of the lake. Perhaps upward diffusion of alkaline interstitial waters from the calcareous sediments beneath maintained a fairly high pH in the sediments above the color change and caused dissolution of diatom frustules. At 14 cm depth this influence may have ceased due to the depth of organic sediment deposited above the calcareous sediments, and thus diatoms were able to be preserved in the upper portion of the core. The diatom counts carried out in this portion of the core are summarized in Table 14, with a diatom count from the top of the frozen short core for comparison of species composition. The correlation between the diatom stratigraphy of the shallow short core and that of the frozen short core, as indicated in Table 13, is based mainly on the fairly high numbers of Melosira italica frustules counted in the shallow short core. This seems to indicate that the whole portion of the shallow short core in which diatoms are preserved corresponds in time to zone (c) of the frozen short core, since Melosira italica increases in abundance in this uppermost zone of the frozen short core.

Sallie Lake

1) Not under the influence of pollution (40-57 cm)

The high percentages of Melosira italica and M. granulata seem to indicate oligotrophic-mesotrophic conditions, since Melosira italica prefers oligotrophic conditions and M. granulata is generally favored by eutrophic conditions, according to the literature sources cited above.

2) Under influence of pollution (0-40)

Zone (a), which begins with the darkening of sediments at about 40 cm depth, seems to represent mesotrophic conditions in

Sallie Lake, with dominance of Stephanodiscus astraea var minutula. Pollen analysis of this core indicates that this change occurred at the time when Ambrosia pollen increased (about 1880, the time of land settlement), suggesting that the source of pollution was agricultural runoff. Zone (b) apparently represents more eutrophic conditions, with dominance of Fragilaria crotonensis, F. capucina var mesolepta, and Stephanodiscus astraea var minutula. This stratigraphic change in diatom populations which took place in the upper several centimeters of the sediment presumably resulted from the recent inflow of sewage wastes into the lake, starting in recent years.

Lake Washington

1) Not under influence of pollution

During the times when sewage from Seattle was not entering Lake Washington prior to the establishment of the city, and in the years 1930-1941, when sewage was diverted from the lake, the diatom populations of the lake were dominated by Stephanodiscus astraea var minutula and Melosira italica (Stockner and Benson, 1967). The contemporaneous occurrence of Asterionella formosa, which commonly occurs in the plankton of mesotrophic-eutrophic water, suggested to these authors that Lake Washington at this time was not truly oligotrophic.

2) Under influence of pollution

Sewage from Seattle was discharged into Lake Washington from the time of the establishment of Seattle until 1930, and from 1941 until the present. The dominance of Fragilaria crotonensis and F. construens during these periods suggests eutrophic conditions in Lake Washington.

The general conclusions concerning the trophic status of diatoms based on the studies in Elk Lake, Sallie Lake, and Lake Washington are:

Oligotrophic - Centrales other than Stephanodiscus astraea var minutula

Mesotrophic - Stephanodiscus astraea var minutula

Eutrophic - Fragilaria species

3. Distribution of fossils in surface sediments

Little information is available concerning the horizontal distribution of fossil diatom frustules in lake sediments. Pennington (1943) has shown that cores from deep water in Windermere are dominated by attached species. Merilainen (1969) has analyzed sediment samples from different parts of Lake Valkiajarvi, and found that planktonic species are abundant in the samples from the littoriprofundal and from the profundal zones. A similar study is at present being carried out in Elk Lake by John Bradbury. A comparison between the species composition of the sediments from the uppermost samples in the shallow short core and the frozen short core from Elk Lake show considerable differences in the percentages of planktonic and littoral species (Table 14). In the shallow-water short core, the percentage of littoral diatom frustules in the sample 4 centimeters below the sediment surface is 36.5%, compared to a percentage of 15.5 in the sediment surface sample of the frozen short core, which was obtained in the deepest hole of Elk Lake. These data seem to correspond to the observations discussed above, and it may be suggested that diatom frustules are not uniformly distributed by water circulation throughout the lake.

| | Shallow-water Short Core (SCs) | | | Frozen Short Core (SCf) |
|--|--------------------------------------|----------------|----------------|-------------------------------|
| Depth of sample below surface: | 4 cm | 9 cm | 14 cm | Surface |
| <u>Tabellaria fenestrata</u> | 29 | 31 | 23 | 16 |
| <u>Asterionella</u> sp. | 1 | 1 | - | 18 |
| <u>Cyclotella kützingiana</u> | 2 | 2 | - | 2 |
| <u>C. bodanica</u> | 4 | 12 | - | 11 |
| <u>C. stelligera</u> | - | - | - | 6 |
| <u>Fragilaria pinnata</u> | 81 | 19 | 24 | - |
| <u>F. pinnata</u> var <u>parallela</u> (?) | - | 5 | 3 | - |
| <u>F. vaucheriae</u> | 32 | 16 | 28 | 6 |
| <u>F. construens</u> | 21 | 10 | 10 | - |
| <u>F. construens</u> var <u>binodus</u> | 1 | 6 | - | - |
| <u>F. crotonensis</u> | 10 | 14 | 12 | 5 |
| <u>F. brevistriata</u> | 41 | 36 | 36 | - |
| <u>F. capucina</u> var <u>mesolepta</u> | - | 7 | 6 | 4 |
| <u>Melosira italica</u> | 10 | 23 | 45 | 28 |
| <u>M. granulata</u> | 4 | - | 3 | - |
| <u>Stephanodiscus niagarae</u> | 7 | 10 | 17 | 7 |
| <u>S. astraea</u> var <u>minutula</u> | 5 | 6 | - | 11 |
| <u>Synedra</u> spp. | 6 | 18 | 11 | 5 |
| Others (70 species, mainly littoral) | 146 (36.5%) | 184 (46.0%) | 182 (45.5%) | 31 (15.5%) |
| Total | 400 | 400 | 400 | 200 |

Table 14. Diatom counts of shallow-water short core and top of the frozen short core.

4. Stratigraphy

Stratigraphic studies of diatoms have been carried out in several European localities, including Esthwaite Water (Round, 1961), Kentmere Valley deposits (Round, 1957) and Neasham late-glacial deposits (Ross, 1952). A study of lateglacial diatoms of Kirchner Marsh in southeastern Minnesota has been recently published by Florin (1970) and a study in Pickerel Lake in South Dakota by Haworth (1971). In the present study of Elk Lake, diatom stratigraphy has been studied in core 69-6 (Plate 12) and in the two short cores (Plate 14 and Table 14). Diatoms were not preserved in shallow-water cores below a depth of about 15 cm of sediment. The continuous record of diatoms preserved in the 69-6 core is believed to be the result of fairly low pH conditions in the deep hypolimnion, whereas high pH in the shallow cores caused the dissolution of diatom frustules. Complexes of silicon with oxygen, which are an important constituent of the cell walls of diatoms, are known to be soluble in alkaline conditions (Chemistry Handbook).

In the studies of core 69-6 and the frozen short core, absolute diatom influx (diatoms/cm³ sediment) and absolute diatom influx (diatoms/cm²/yr) were calculated. These figures are not considered to be very instructive with respect to indicating actual changes in diatom productivity in Elk Lake for two reasons:

- 1) Changes in absolute diatom frequency and influx correspond to changes in lake circulation patterns envisioned on the basis of the observed changes in lamination characteristics of the sediments of core 69-6. Absolute diatom frequency and influx are high before the Quercus-Ostrya period when lake circulation was presumably strong,

carrying littoral and planktonic diatoms into deep waters. Above the beginning of the Quercus-Ostrya zone in the sediments, absolute diatom frequency and influx decreased considerably, presumably because of poor circulation of Elk Lake. This seems to correspond to the observations made by M. Davis (pers. comm.) with respect to deposition of pollen in lake sediments. In a stratified lake, light pollen grains are deposited mainly in the littoral zone, since water movements within the epilimnion keep them in suspension and prevent them from settling into hypolimnetic waters.

2) Changes in absolute diatom frequency and influx are not in accord with probable productivity changes suggested by changes in diatom species in the cores, i.e. absolute diatom frequency and influx decrease at the beginning of the Quercus-Ostrya zone when changes in diatom species and in species of other aquatic organisms suggest an increase in productivity in Elk Lake. However, in the frozen short core, the increase in absolute diatom frequency and influx does correspond to the time of eutrophication.

The diatom stratigraphy of the Elk Lake cores will be discussed with respect to the faunal units which have been recognized in the Elk Lake cores:

Unit C - This faunal unit corresponds to lower and middle Quercus-Gramineae-Artemisia pollen zone in the pollen diagram of the 69-6 core. The base of the 69-6 core is assigned to faunal unit C on the basis of correlation with other cores by pollen analysis, which places the lowest samples in the lower to middle Quercus-Gramineae-Artemisia zone. The diatom assemblage was dominated by Stephanodiscus astraea var minutula, which suggests mesotrophic lake

conditions.

Unit D - This faunal unit corresponds to upper Quercus-Gramineae-Artemisia and lower Quercus-Ostrya periods in the pollen diagram of the Elk 69-6 core. A decrease in the predominance of Stephanodiscus astraea var minutula and an increase in the percentage of other Centrales, including Stephanodiscus niagarae, Cyclotella kützingiana, C. compta, C. stelligera, and Melosira italica, takes place in the upper Quercus-Gramineae-Artemisia zone. This diatom change suggests decreasing productivity in Elk Lake at this time, according to the interpretation of the trophic status of Centrales discussed above.

Unit E - Several changes in diatom populations in Elk Lake seem to have taken place during this faunal unit, representing the period from the middle Quercus-Ostrya zone to the present. In the Quercus-Ostrya zone, the Centrales percentage begins to decline, while Pennales, especially Asterionella formosa and Fragilaria crotonensis, increase in percentage. The decline in Centrales percentage is demonstrated most clearly by the abrupt decrease in Melosira italica and later in Cyclotella kützingiana, while Stephanodiscus astraea var minutula maintains fairly high percentages. The increase in percentage of Pennales, especially of Fragilaria crotonensis, continues into the following period, reaching a peak in the lower Pinus strobus zone. In the upper part of the Pinus strobus zone, the Pennales decline as the Centrales, especially Stephanodiscus astraea var minutula, again assume dominance. These diatom changes in unit E suggest that eutrophication began in Elk Lake at the time of the Quercus-Ostrya zone, reaching a peak in the lower Pinus

strobis zone, and that the lake reverted to mesotrophic conditions in the upper Pinus strobis zone. The recent eutrophication of Elk Lake by human activities, designated as unit E' (0-53 cm in core SCf), was discussed under the ecology of diatoms.

SUMMARY AND CONCLUSIONS

The investigation of Elk Lake involves three main areas of study — ecological studies, studies of distribution of fossils within the lake by water movements, and stratigraphic studies. The main objective of the work is to interpret the limnological history of Elk Lake through the stratigraphic analysis, with the studies of ecology of living organisms and fossil distribution in surface sediments being designed to aid in the interpretation of fossil remains identified in the sediments. The following summary of the major conclusions in each of the three areas of study may be given:

1. Ecological studies

The ecological studies of aquatic organisms carried out in Elk Lake and in Green Lake are designed to supplement the ecological information available in the literature. In the studies of chironomids, molluscs, aquatic macrophytes, and diatoms, the conclusions derived from the present studies correspond quite well with the information cited in the literature. Inasmuch as less information is available in the literature concerning ostracod ecology, the main goal of the ecological studies is to make a contribution to this subject. An attempt is made to answer two of the main questions in ostracod ecology, namely the degree of community development and the relative importance of various ecological factors in controlling the distribution of ostracods. In Elk Lake, two ostracod communities are identified according to the 50% rule: a plant-associated community composed mainly of two ostracod species, Cypridopsis vidua and Cyclocypris sp., and a benthic ostracod community composed of many species (about 17). In Green Lake only the benthic ostracod

community was studied. Several subcommunities, corresponding quite closely to different habitats, are recognized in both lakes. The main factor determining the separation of ostracods into the two communities seems to be simply the differences in the ability of various ostracod species to swim actively, for active swimmers are associated with aquatic macrophytes, and poor swimmers are restricted to the sediments. The main factors controlling the differentiation of subcommunities within the benthic ostracod community seem to be sediment character in the relatively shallow areas and oxygen content of the bottom waters in deeper areas. The same conclusion is reached independently in the study of ostracod stratigraphy in shallow and deep-water cores.

2. Studies of fossil distribution in surface sediments

A study of the distribution of fossils in surface sediments of Elk Lake was carried out in order to determine the extent to which organisms are transported by water movements from their living habitat, either while living or after death. The main conclusions reached in this study were:

- 1) Many fossil organisms living in relatively shallow water are transported offshore by wave-induced currents and deposited in a shell zone located at a depth of about 2-4 m at the northern end of Elk Lake and considerably deeper (about 10 m) at the southern end. The deposition of fossils and precipitated marl in this fashion resulted in the formation of a bench or terrace in shallow waters around the periphery of Elk Lake. Such a shell-zone distribution was noted for some fossil molluscs, seeds and spores, and ostracods.
- 2) Most benthic organisms living in relatively deep water seem

to undergo little transportation by water currents but are preserved in situ. This conclusion was reached on the basis of the close correspondence between depth-distribution ranges of living and fossil ostracods and chironomids in deep-water sediments, below the influence of waves and of offshore currents associated with wave activity. Bottom currents and overturn of the lake seem to be relatively ineffective in redistributing these organisms from living habitats.

3) Some littoral organisms seem to be transported to some extent into deeper waters, probably by water movements in the epilimnion or by floating on the water surface. Some ostracods, especially actively swimming species, seem to be carried out quite frequently, probably as "adventitious planktonts". Very few littoral molluscs float out and are deposited in deep-water sediments. The limited redistribution of diatom frustules is probably a result of epilimnetic currents. Seeds having various adaptations for floating are quite frequently found in deep-water sediments.

3. Stratigraphic studies

In the stratigraphic studies of nine Elk Lake cores, five faunal units are recognized, characterized by distinctive faunas of ostracods, chironomids, and molluscs, as well as by distinctive sediment types in most cases. The stratigraphy of each group of organisms is discussed in terms of these five units. The general interpretations of the paleolimnology of Elk Lake based on these studies are as follows:

Unit A - Herb? pollen zone and lower Picea zone

This unit presumably represents the period in which Elk Lake

was receiving clastic sediments, probably derived from the erosion of outwash deposits of the St. Louis sublobe, as indicated by the occurrence of shale fragments. Relatively little information concerning limnological conditions in Elk Lake at that time can be derived from the few fossils of chironomids, molluscs, and seeds found in the cores, but several of the ostracod species found in this unit were identified by Staplin (1963a; 1963b) in his study of Pleistocene ostracods of Illinois and presumably are cold-hardy species. The unit ends very abruptly as finer organic sediments replace the clastic sediments near the end of the Picea period.

Unit B - Upper Picea pollen zone to top of Pinus banksiana/resinosa-Pteridium pollen zone. Fossils of chironomids, molluscs, and ostracods suggest that Elk Lake was oligotrophic during this period.

Unit C - Lower and middle Quercus-Gramineae-Artemisia pollen zone. The stratigraphy of chironomid, mollusc, and ostracod fossils suggest a lower oxygen content of bottom waters of Elk Lake in this period than in the preceding period. This may indicate increased productivity in Elk Lake. The boundary between units B and C corresponds closely with the boundary between the Pinus banksiana/resinosa-Pteridium and Quercus-Gramineae-Artemisia pollen zones, which seems to suggest that the proposed lake productivity change is associated with the change in terrestrial vegetation, perhaps by a nutrient increase or rise in pH. It may also be suggested that the proposed eutrophication is more directly the result of the climatic amelioration that produced the vegetation change.

Unit D - Upper Quercus-Gramineae-Artemisia pollen zone to middle Quercus-Ostrya pollen zone. The fossil stratigraphy of

chironomids and molluscs shows little change from the preceding unit, but all ostracod species in the deep-water cores exhibit a very abrupt decline in abundance at the base of this unit. A postulated decrease in the productivity of Elk Lake at this time is supported by the abrupt lightening of sediment color in cores 69-2, 69-3, and 69-5 at the base of the unit.

Unit E - Middle Quercus-Ostrya pollen zone to present. The stratigraphy of chironomids, molluscs, ostracods, and diatoms all suggest an increase in productivity of Elk Lake at the base of this unit and persisting until the present. The olive color of sediments of this unit in almost all of the cores, as well as the increased organic matter percentage and higher sedimentation rates, especially in shallow water as the marl terrace began to build up, seem to confirm this suggestion. It is suggested that the eutrophication of Elk Lake in the middle Quercus-Ostrya period may have been related to the establishment of the Quercus-Ostrya forest in the watershed.

Unit E' is recognized in the two short cores studied. The unit is delimited by an abrupt darkening of sediments in the shallow-water short core (SCs) and by a change from fine laminations to broad, poorly defined bands in the deep-water frozen short core (SCf). Stratigraphy of chironomids, ostracods, and diatoms suggests abrupt eutrophication at the base of the unit, followed by partial reversion to pre-disturbance conditions. Pollen analyses of these cores suggest that the eutrophication began about the time that the extensive lumbering activities in Itasca State Park were carried out, from 1917 to 1919. It is suggested that eutrophication of the lake resulted from the inwash of soil as the 1-m dam built at the outlet of Elk Lake at Chambers Creek in 1917 raised the water level.

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Key: * Seeds and molluscs counted in 5 cc samples
M - adult male; F - adult female; Im - immatures
1, 2, 3 - size classes of immatures, 1 largest

[illegible]

